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Modelling eco-evolutionary dynamics of species' traits in size-structured ecosystems

by

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"A model is a simplification or approximation of reality

and hence will not reflect all of reality.

George Box noted that "all models are wrong, but some are useful."

While a model can never be "truth," a model might be ranked from very

useful, to useful, to somewhat useful to, finally, essentially useless."

– K. P. Burnham and D. R. Anderson

UNIVERSITY OF TASMANIA

Abstract

Modelling eco-evolutionary dynamics of species' traits in size-structured ecosystems

by Romain FORESTIER

Human impacts on natural systems are driving rapid ecological and evolutionary changes. In the ocean, we know that fishing and climate change are affecting the functional traits of species and restructuring ecosystems. However, the extent to which evolutionary adaptations can buffer ecosystems against these impacts is not well understood. This information is needed to improve knowledge of how ecosystem function and biodiversity are being affected by a rapidly changing ocean.

This thesis is centred around the introduction of evolutionary dynamics into trait-based models. Trait-based models capture functional biodiversity of ecosystems by resolving traits within and across multiple species. However, current trait-based models do not allow for traits to change through adaptation and natural selection on the same time scales as ecological processes. Yet there is growing recognition that evolution can act on the same time scales as ecology.

The key aim of the thesis is to extend trait-based size spectrum models, widely used to assess impacts of fishing and climate change on fish communities, by exploring how species adaptation can alter population and ecosystem responses to environmental and human-induced change. I develop an eco-evolutionary simulation model that introduces new phenotypes into a dynamic trait- and size-based community model. I then apply the model to three theoretical case-studies, each focusing on the adaptation of a key trait thought to be under strong selection from external

drivers.

Firstly, I explore the case of fisheries induced evolution or how fishing drives the adaptation of maturation size in fish. Here, the study confirms previous empirical findings and single-species based predictions that size selective fishing will generally drive a reduction in maturation size for large fish species. However, due to interacting forces of predation and competition, this effect was not found for small species and was sometimes reversed for medium-sized species.

Secondly, I examine species' thermal performance as an adaptative trait under a warming climate. This study shows that in the short-term ($\sim$ 50 years), under a projected 'high emissions' climate scenario, marine species' phenotypic diversity helps to buffer against warming temperature by species slowly adapting towards more generalist thermal strategies. However, at the projected rate of warming of $3.5°C$ per 100 years over 200 years of simulation, phenotypic diversity eventually collapsed as as adaptation could not keep up with rapid change and specialised phenotypes disappeared.

Thirdly, I investigate the driver of food limitation to explore how feedbacks between predation and competition might lead to species-specific differences in the relative prey size preferences of fish. This chapter asks why some large marine fish (e.g. large planktivores) feed on much smaller prey relative to their own body size compared to others (e.g. predatory sharks). The model predicts that low resource availability drives an adaptation towards smaller relative prey size and that apex carnivores, who feed on relatively larger prey, only emerges as an alternative strategy if enough energy is available to transfer up the food webs.

In summary, the model developed in this thesis has been used to show that there is significant scope for adaptations in size-structured multispecies systems. Some of the general patterns predicted by the model were consistent with macroecological patterns for fish. Future work

would be needed to develop and test the model to support biodiversity policy and ecosystem-based management.

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List of Abbreviations

AD Adaptive Dynamics

CAS Complex Adaptive System

FIE Fisheries Induced Evolution

GS Generalist/Specialist

PPMR Predator:Prey Mass Ratio

QG Quantitative Genetics

TO Temperature Optimum

Chapter 1

Using evolutionary dynamics to capture biodiversity in models

This century has been marked by global environmental change and regime shifts in ecosystems worldwide (Gamfeldt et al., 2015). Marine ecosystems in particular are subject to overexploitation, species invasion, pollution and eutrophication (Smith, 2003; Halpern et al., 2008). Oceans are also becoming warmer and more acidified (Hoegh-Guldberg and Bruno, 2010; Burrows et al., 2011; Doney et al., 2012). Unfortunately, these impacts have consequences for the wellbeing and livelihoods of billions of peoples that depend on the oceans and the critical services they provide (e.g. food, tourism/entertainment, climatic buffer, waste assimilation) (Millennium Ecosystem Assessment (Program), 2005; Barbier et al., 2011). It is well determined that biodiversity is linked to ecosystem function and the provision of ecosystem services (Palumbi et al., 2009; Cardinale et al., 2012; Balvanera et al., 2014), and therefore it is essential to understand the consequences of biodiversity loss in the context of ecosystem function (Hooper et al., 2005; Naeem et al., 2012).

Over the past century, a variety of concepts and models have been applied to better understand the relationships between biodiversity and ecosystem structure, function, and dynamics (Lindeman, 1942; Pimm and Rice, 1987; May, 2001; Brose et al., 2016). Trait-based models have been important in developing an understanding of the links between functional traits and the structure and dynamics of communities and ecosystems (Mcgill et al., 2006). Switching the focus of

models (and scientists) from species identity to functional traits provides a fruitful way of looking at communities through the lens of function and functional groups.

The overall aim of this thesis was to develop trait-based models to capture biodiversity changes in marine ecosystems by considering these systems as complex adaptive systems. Here, I adopt a trait-based modelling approach to provide new understanding of the consequences of changes in traits through time in response to different drivers of change, with a focus on marine ecosystems. This introductory chapter begins by drawing on the wider historical developments at the interface of community, ecosystem, and evolutionary ecology – including the concepts of complex adaptive systems (Levin, 2003) and eco-evolutionary feedbacks (Matthews et al., 2011). I then discuss how trait-based models, particularly trait-based size spectrum models, have been developed to capture eco-evolutionary feedbacks, and highlight the key gaps and potential advantages of this approach in representing complex adaptive systems. This is followed by an outline of the thesis structure, including the modelling approach and specific research questions.

1.1 How can traits inform ecology and biodiversity?

During the second part of the 20th century, ecologists aimed to answer the question: "Why is there so much diversity?" (Hutchinson, 1959). Since Darwin so clearly laid out his ideas around a theory of evolution (Darwin, 1859), ecologists have looked to explain how environmental and other pressures shape species over time, essentially asking how evolution works – Jean Baptiste Lamarck's presentation of the ideas of transformisme may be the earliest scientific evolutionary theory, but the concept of species change had been discussed as far back as Empedocles (ca. 495–35 BCE). This thinking was motivated by observations that even within regions/ecosystems with the same physical properties (temperature, pressure, humidity), one can find totally different species – which leads to the question, "does history play a role in speciation?".

Ecosystems are non-linear dynamical systems with historical dependency and stochastic elements. This has led to the realisation that when such systems are run repeatedly from the same set of initial conditions multiple outcomes and reactions are possible (Strogatz, 2000). As a

result, generalisable knowledge is only possible if we look for larger patterns across the different instances to develop understanding of systemic phenomena (Paine, 2010). This approach contrasts with the reductionist approaches that characterised large bodies of science through parts of the 20th century (Raffaelli, 2007). Ecology is a frustrating science in that it simultaneously requires this "big picture view" to find the "laws" and "general principles" while linking back to the constituent parts, the smaller scales, which can influence the specific outcomes in particular instances (Lawton, 1994, 1999; Poisot et al., 2016).

Using traits allows modelling simple interactions at the individual level that have meaningful effect on trends at the ecosystem level (Carmona et al., 2016). Traits and their variation among individuals lead to a diversity of physiological, behavioural and ecological processes, creating intra-population variation (Bolnick et al., 2003). This variation often has an important ecological and evolutionary impact. Therefore, traits are at the intersection between evolutionary biology and ecosystem science (Matthews et al., 2011).

Functional traits are components of an organism's phenotype that influence ecosystem level processes (Petchey and Gaston, 2006). Using functional traits instead of species identity is a powerful means of investigating biodiversity in complex ecosystems as it focuses on ecological functionality (core to ecosystem dynamics), rather than taxonomy (i.e. one can reduce a large number of species into key functional traits that can describe ecosystems). Previous work (Fulton et al., 2003) has shown that capturing ecosystem function is fundamental to ecosystem model performance. Moreover, a trait focus allows for the exploration of critical ecological concepts such as the notion of keystones species and redundancy, where some species are more important (because of key traits), and the loss of species can be mitigated by others with the same traits, respectively (Hooper et al., 2005).

Traits have been used in community ecology with varying levels of success but in some cases have shown to be very effective representations of community structure (Follows et al., 2007). These traits (e.g. size, feeding behaviour) determine the functional roles that individuals play, and therefore determine the functional diversity of an ecosystem, which is a key component of biodiversity. However, the structural complexity of communities was, and still is, very

challenging to represent and has led to many disparities in the way different research groups have used traits in exploring ecological patterns and processes (such as changes in abundance and trophic interactions through space and time) and evolution (Lawton, 1999; Poisot et al., 2015).

Focus on traits can also help to focus on the dynamic nature of interactions among ecosystem components (species, populations), rather than on fixed species characteristics. Natural ecosystems consist of individuals continuously reacting to their changing environment, in turn driving their adaptation. Over time, phenotypic distributions in communities shift in response to environmental change, which, in turn, changes the magnitude or expression of ecosystem processes and consequently ecosystem structure (Díaz et al., 2013). In other words, there arise feedbacks between environment and evolution (Matthews et al., 2016). Being at the interface of both, traits can help model this feedback. Hence trait-based models are a useful tool for understanding the role of biodiversity in ecosystem functioning. Some have argued that trait diversity could even be a better proxy for ecosystem function than species biodiversity (Norberg et al., 2001).

Capturing this dynamic nature of ecosystems in relatively simple modelling tools has been one of the major challenges of evolutionary ecology. Adaptive trait model is one of possible approaches, where traits are allowed to change through time to both follow and drive the changing nature of ecosystems (Norberg et al., 2001; Tilman et al., 2001). In this sense, ecosystems are an example of complex adaptive systems, where local interactions and selection processes drive properties at higher levels which can feed back to influence local interactions and selection processes.

Using traits as a lens, it is possible to link into a number of important dynamic processes and ecological theories. Holland (1992) Complex Adaptive Systems theory (CAS), applied to ecology, is a conceptual framework offering a dynamic view; one in which fixed values for species composition of modelled groups (and associated traits) are replaced with rules that are a function of long term (e.g. species) and short term (typically individual) histories, embracing the adaptive capacity of natural systems. Many different definitions have been proposed since its first conceptualisation, but three main characteristics of CAS were summarized by Levin (2003):

1. Diversity and individuality of components (e.g. individuals)
2. Localized interactions among those components
3. An autonomous process that uses the outcomes of those interactions to select a subset of those components for replication or enhancement (e.g. adaptation)

In other words, CAS are systems where local interactions between the smallest components (e.g. individuals) will lead to changes at higher levels of biological organisation (populations, communities) and larger scales (spatial, time), and the emergence of self-organization of complex entities without outside influences.

The adaptation allowed by CAS can be divided in two linked processes: the emergence of pattern in a system of fixed entities; and the continual appearance of new entities (Levin, 2003). Models based on CAS aspire to understand ecosystem dynamics in terms of diversity and selection. They use distributions of traits in communities as input and subject those communities (and their trait expression) to change to study the impact of local adaptations on higher level processes. One of the main aspects of CAS is non-linearity, leading to different possible trait dynamics and history (path) dependency. CAS models aim to differentiate the role of the environment from trait dynamics in the development of ecosystems through time (Levin, 1998). Understanding the relationship between environment and traits helps create a predictive capacity regarding the response of communities to perturbations. Such models would be useful to investigate contributions to ecosystem dynamics and functioning that are determined by adaptation under 'natural' environmental and human induced change. They would allow us to ask whether evolution buffers ecosystems from change, or sees ecosystems hover at the edge of chaos.

In the following section I examine the case for using trait-based models in the context of adaptation and biodiversity change.

1.2 Trait-based models as tools for understanding adaptation and biodiversity change

In an effort to find general rules in community ecology, Mcgill et al. (2006) more clearly (re)defined what a trait is and how to use it; they did this by drawing on four research themes: traits, environmental gradients, performance currencies, and interaction milieu. They concluded that for traits to be useful in community ecology, traits have to be a quantitative representation of an individual's phenotype. They should be continuous units, meaning traits can be placed on a smooth scale across individuals rather than lumped into discrete classes. And finally, traits should be able to be measured, enabling comparison among individuals (Mcgill et al., 2006). In summary, any organism's characteristic can be called "trait" but if we want to be able to compare studies, trait-based studies need to follow the "quantitative/continuous/measurable" rule, as even with this clear definition of a trait, there is still the need for a common framework for modelling functional diversity using traits. To date each scientist has typically developed their own specific model, making it difficult to compare among studies if the traits used do not follow the above-mentioned rules (Webb et al., 2010).

As mentioned in the previous section, traits provide a fruitful approach to capturing individual, community and ecosystem level dynamics because they can summarise critical aspects of diversity. Therefore, they will influence individual performance, community structure and function, biological diversity, trophic interactions and ecosystem processes (Litchman and Klausmeier, 2008). As a result, trait variation among individuals, populations and communities is fundamental in biodiversity and niche construction studies (Bolnick et al., 2003). Trait-based models use the value of functional traits and their variation to ultimately describe ecosystem processes (Litchman and Klausmeier, 2008; Hartvig et al., 2011). Using traits allow to focus on a few characteristics, making models more manageable, but while describing ecosystems with a few key traits, we need to be confident in which traits we choose to capture all key properties of said ecosystem. Moreover, trait variation can be influenced by a range of factors, such as evolution through time, environmental feedback, or even trade-offs among traits (Zhang et al., 2015;

DeLong and Gibert, 2016).

1.2.1 Trade-offs enable adaptive strategies

Even when using one trait in models there is already the potential to obtain powerful results in terms of realistic model outputs that can be instructive about real world processes (Benoît and Rochet, 2004; Loeuille and Loreau, 2005; Hartvig et al., 2011). Yet, in reality traits in organisms always interact, and accounting for these interactions can improve model realism, by introducing trade-offs among traits and preventing any one trait reaching unrealistic values (Pavličev and Cheverud, 2015; Mathot and Frankenhuis, 2018). One of the main objectives in community ecology is to understand trade-offs between traits, as using multiple traits will often lead to dynamics unobtainable when considering a single trait in isolation (Chevin et al., 2010). These trade-offs allow for the emergence of complex and non-linear strategies/dynamics in models (Litchman et al., 2007). Interestingly, these kinds of results arise commonly regardless of the original motivation or the approach taken to integrate multiple traits into models (i.e. regardless of the aspect of biodiversity the modeller had in mind, Ghalambor et al. 2003; Scheiter et al. 2013; Kopp and Matuszewski 2014; Hunt et al. 2015; Falster et al. 2015; DeLong and Gibert 2016.

1.2.2 Trait representation

An advantage of trait-based models is the simplified representation of many species through their traits, enabling global estimation of ecosystem structure (Harfoot et al., 2014), food-web interactions (Williams and Martinez, 2000; Gravel et al., 2016; Albouy et al., 2019), and dynamics (Hartvig et al., 2011; Brose et al., 2016). Traits enable the modeller to represent individuals by their function, allowing for the representation of entire food webs via differentiation in terms of one trait; meaning a lot can be done with relatively low computing power.

Using a trait-based model means the modeller can capture differences between species (and even individuals within those species) on their traits. Hence the approach emphasises functional

biological principles and processes (e.g., body size scaling, thermodynamic laws). This simplifies computationally expensive attempts to explicitly define unique parameters for each and every species (Bruggeman and Kooijman, 2007). For example, allometric equations that link species parameters to their body size (example of trait) have been used to reduce the number of parameters in models (Yodzis and Innes, 1992).

A cornerstone of ecological modelling is to represent individual to ecosystem-level processes through equations. Trait-based models specifically take traits as arguments (Desjardins-Proulx et al., 2019) as opposed, for example, inputting 'who eats whom' and the strength of interactions between predators and prey (Christensen and Walters, 2004). Mechanistic equations enable the processes of predator search, encounter and selection and consumption prey to all be described and depend on the traits of predator and prey (e.g. individual and asymptotic body sizes, Andersen 2019). The choice of trait is critical, and the chosen traits are the ones governing organisms' functions or the ones impacting ecosystems' functions. Some traits are "super-traits" (e.g. individual body size, maturation size) because they represent many different processes, and these traits can be used to approximate other traits of an individual or species in a model. These super-traits have been well studied for a number of organisms that have been the subject of large empirical syntheses in terrestrial and aquatic ecology, (e.g. body size, Peters and Peters 1986; Brose et al. 2006b; Jones et al. 2014; metabolic rate, Brown et al. 2004; predator:prey mass ratio, Barnes et al. 2010; Brose 2019; thermal response Dell et al. 2013; dispersal/establishment in reefs Madin et al. 2016). Some of these compilations are species or taxa oriented and as a result do not capture the full scope of ecosystems since entire functional groups can be missing. Furthermore, the use of species' mean traits can often mask intraspecific variation and change in traits. Dynamic evolutionary and ecological processes affecting traits can also lead to changing ecosystem processes, such as biochemical cycles (Litchman et al., 2015). Therefore, extant data can become outdated if they are species focussed because they are unlikely to adequately capture changing ecosystem properties. Combined use of trait-based models and data offer a means of capturing this generality – as species' traits change, the overarching trait-based patterns and equations can help to provide new parameters and predictions.

1.2.3 Trait-based size spectrum models: intra and interspecific traits

Community size spectrum models focus on how the super trait "individual body size" governs biological rates (metabolism, growth, reproduction) and feeding interactions without using species identity. They were originally conceptualised by Platt and Denman (1977) following empirical observations of marine biomass size spectra of Sheldon and Parsons (1967). They are deterministic and dynamic models which, through size-based mechanistic processes, recreate a size spectrum (the abundance of biomass density of all individuals in a community body sizes) and project its variation through time. The system dynamics are obtained by solving the McKendrick (1926); von Foerster (1959) partial differential equations (Benoît and Rochet, 2004; Law et al., 2009; Blanchard et al., 2009).

More recent trait-based size spectrum models extend this earlier approach by approximating species within the size spectrum using the additional trait of asymptotic size (Andersen and Beyer, 2006). These models track abundance and biomass at size through time both within and across species and capture the physiology and food-web interactions within and between species (Hartvig et al., 2011; Andersen, 2019). Using size spectra, with larger animals feeding on smaller ones, one can plot the biomass of individuals grouped by their body size, and quickly explore the effect of perturbations on ecosystem structure and dynamics, such as trophic cascades or decline in large organisms (see reviews by Andersen et al. 2016a; Guiet et al. 2016). Using body mass also makes it easier to compare model results with empirical data (Brännström et al., 2012). Consequently, a good start for modelling studies involving multiple traits is to begin with body size, add new traits, and then explore trade-offs with body size. In his framework, Boukal (2014) added spatiotemporal overlap between individuals and prey/predator encounter as traits. His use of these three traits leads to additional effects on the structure and stability of the modelled food web, allowing for the evaluation of the impact of different traits on the ecosystem. The flexibility of different traits and their parameterisation has led to explorations of how different combinations of parameters, such as the strength of coupling between species or different species' maturation size, lead to coexistence in these size-structured food webs (Rossberg, 2012; Hartvig and Andersen, 2013; Brose et al., 2016).

1.2.4 Traits in the context of impacted and evolving marine ecosystems

Like most marine ecosystem and food web models, the traits used in size spectrum models are typically fixed; they use size at maturation, asymptotic body size, and feeding parameters that describe size-dependent species' or individual-level traits that do not change through time (but see below). However, selective forces are continuously affecting these traits. Even in the absence of major human impacts, predation has long been recognised as a selective force affecting evolution in ecosystems (Darwin, 1859; Abrams, 2001). In aquatic systems, fisheries induced evolution is known to drive major changes in maturation size and age of fish (Audzijonyte et al., 2013b; Heino et al., 2015; Hutchings and Kuparinen, 2020). Similarly, warming associated with climate change is expected to act in a similar way as fisheries on body sizes (Waples and Audzijonyte, 2016), but much depends on the details of thermal preferences, adaptation and interactions among other organisms – all simultaneously exposed to different forces of selection! Given the combination of changes that ecosystems are undergoing combined with the fact that that rapid evolution is now considered to be ubiquitous (Ellner, 2013; Matthews et al., 2016; Beckerman et al., 2016), it is crucial that these processes are better represented in models.

In the section below, I provide a brief background on eco-evolutionary modelling, how this approach has been used so far in trait-based size spectrum models, and what further developments are needed.

1.3 Eco-evolutionary dynamics

There are a range of methods in which evolutionary processes have been captured in ecological models. Roughgarden (1971) was among the first to introduce a temporal gradient impacting variation in density-dependent trait distributions. Since then, essentially three methods have been developed to represent trait evolution in an ecosystem (Abrams, 2001). First, there is Quantitative Genetics (Taper and Chase, 1985; Taper and Case, 1992; Abrams and Matsuda, 1997), which takes into account genetic processes using loci (which is useful when explicitly modelling sexual reproduction). Quantitative genetics models individuals or groups of individuals, and typically

requires assumptions about heritability of traits (i.e. how much of the phenotypic trait value is determined by the additive genetic variance). The advantage is that it allows to focus on underlying genetic mechanism, but at the cost of often computationally intensive simulations. Second, is the Adaptive Dynamics (AD) approach (Dieckmann and Law, 1996; Metz et al., 1996; Geritz et al., 1997), which eschews genetics for stochastic generation of phenotypical mutations, with each mutation having a small individual effect on the relevant traits. Adaptive dynamics models phenotypic evolution under clonal reproduction (i.e. ignore underlying genetics) and assume a mutation rate far slower than any ecological variations. It is a framework that can be solved analytically and predicts all outcomes possible of mutants' invasion but will model one trait at a time. The third method, Evolutionary Stable Strategy (ESS) (Brown and Vincent, 1987; Vincent and Brown, 1988; Vincent et al., 1996; Cohen et al., 1999) is now encompassed in adaptive dynamics (Diekmann, 2004) as a specific case where adaptation leads to a stable phenotype that cannot be invaded by other strategies. My trait-based approach sits in between quantitative genetics and adaptive dynamics by modelling phenotypic evolution with multiple traits and with same ecological and evolutionary scale. Using traits provides the freedom to model a tractable number of non-static parameters which can change through time. Traits therefore enable realistic but computationally feasible representations of evolution.

The work in this thesis builds on the early output of a new area of research – effectively modelling evolution on ecologically-relevant time scales. Ecosystem structure is determined by the interactions within and across species, including their addition and extinction to the ecosystem. In the 21st century, computation capacity and available data have reached a point where models of evolution have been easier to develop. This has seen several models include evolutionary rules and produce realistic large communities with self-structuring networks. Using a food web model that characterised species by their mean body size, with all species interactions depending on that trait, Loeuille and Loreau (2005) showed that simple ecological rules combined with mutation and selection processes led to the emergence of realistic complex food webs. Later, more complex allometric food web models implemented more than one trait to obtain different life history strategies yielding the emergence of complex networks (Drossel et al., 2004;

Rossberg et al., 2006; Guill and Drossel, 2008) with more dynamical structure through time, allowing emergent species turnover and secondary extinctions (Takahashi et al., 2013; Allhoff et al., 2015).

Trait-based size spectrum models, which resolve intra- as well as inter-specific variation in body size, have also incorporated evolutionary processes to study the adaptation of organisms' traits over long time scales (Andersen and Brander, 2009; Hartvig et al., 2011), including in combination with adaptive dynamics under different forces of selection. For example, Zhang et al. (2015) studied the effects of different types of competition for resources on the maturation sizes in a modelled fish community, showing that competition always lead to trait diversification. Law and Plank (2018) used adaptive dynamics to assess how alternative harvesting strategies might minimise the evolutionary effects of fishing using a dynamical size spectrum model. Other types of physiological or size-structured models have been widely used to combine quantitative genetics and adaptive dynamics to assess impacts of ecological changes on evolutionary processes (Dunlop et al., 2009; Govaert et al., 2019).

All these above size-structured models (except Dunlop et al. 2009) assume a separation of ecological and evolutionary time scales, with fast ecological dynamics to select species and a slow evolution to introduce new ones once the ecosystem is stable. However, as mentioned above, eco-evolutionary feedbacks are increasingly present in the literature (Ellner, 2013; Matthews et al., 2016; Beckerman et al., 2016), meaning that ecology and evolution happen at the same time scale and influence each other.

1.3.1 Eco-evolutionary feedbacks

Eco-evolutionary feedbacks have two requirements. First, ecology and evolution must operate on the same time scale. It has long been assumed that natural selection does not have an effect at short time scale, which increases computational efficiency and allows model to reach equilibrium, but recent research shows that evolution can be rapid (Matthews et al., 2011). Second, these rapid adaptations must be reflected as changes in an organisms 'environment'. Studies show that organisms do modify their environment by altering the community structure and ecosystem

processes around them (Harmon et al., 2009; Pelletier et al., 2009; Bassar et al., 2010). In turn, changing the ecosystem will affect species interactions and their evolutionary history. This feedback loop is at the core of eco-evolutionary dynamics (Fig.1.1). The feedbacks can manifest at multiple ecosystem levels, for example simultaneously affecting cohort parameters, community structure, or food web structure (Pelletier et al., 2009). It is this eco-evolutionary scale that is the focus of the modelling presented in this thesis.

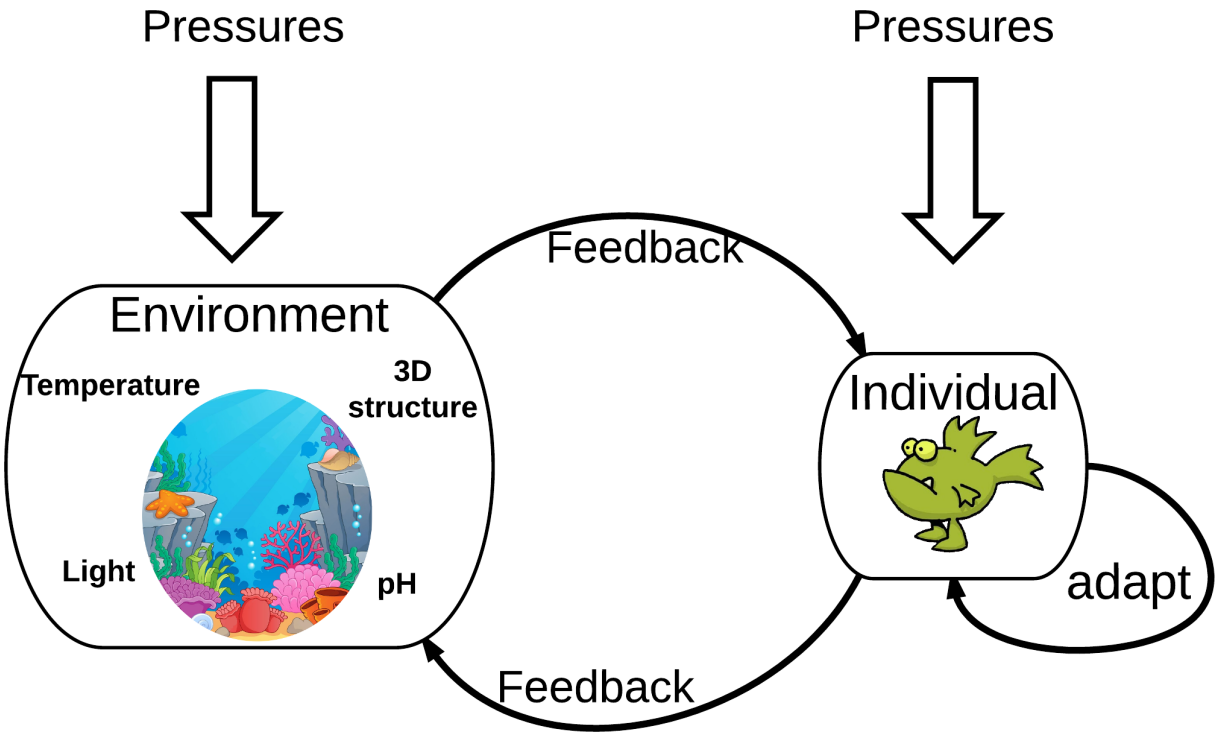

FIGURE 1.1: Concept of feedback cycles in an eco-evolutionary context.

1.4 Structure of the thesis

By putting eco-evolutionary feedbacks into trait-based size spectrum models, I develop an approach that explores the consequences of different pressures on complex eco-evolutionary systems. I focus on marine ecosystems where the human activity of fishing and anthropogenically-driven ocean warming affect the direction of natural selection against a backdrop of other factors such as inter- and intra-specific competition and predation.

To do this, I develop a model that extends the ecological trait-based modelling approach to include evolutionary processes. The model is based on the size structured marine ecosystem

model "mizer" (Scott et al., 2014) and extends it by enabling evolutionary processes (Fig 1.2). "Mizer" manages the ecological processes such as predation/growth/mortality/reproduction and the extension transforms the species into groups of phenotypes (i.e. phenotypic diversity), each phenotype having a slightly different value of the trait being studied. New phenotypes are being continuously added to these species and the less fit phenotypes go extinct due to natural selection, effectively reproducing evolution in the model.

I apply the model to answer three overarching research questions in exploring how dynamics eco-evolutionary changes affect marine ecosystems under a variety of pressures.

Question 1: How do the interacting forces of fishing and predation affect species' maturation size in a complex size-structured community?

In chapter 2, I develop a trait-based size spectrum model and apply it to the question of how species' maturation sizes respond to fisheries-induced evolution when species are also exposed to the selective forces of inter- and intra- specific predation and competition. In theory, we expect fishing as a selective force to select for earlier maturation at smaller body size (Audzijonyte et al., 2013a). This process is called Fisheries Induced Evolution but its effect on ecosystem structure remains debated, since other selective forces such as predation also act on ecosystem structure. Changes in maturation size from fishing and predation have previously been explored with multi-species physiologically structured models (Blanchard et al., 2014; Law and Plank, 2018), but this work assumed separation of ecological and evolutionary timescales.

To avoid this limiting assumption, I developed a model to account for eco-evolutionary dynamics in a physiologically size-structured food web, where new phenotypes are introduced randomly through time enabling dynamic simulation of species' relative maturation sizes under different types of selection pressure.

Question 2 How do species' predator:prey mass ratios (PPMRs) evolve in communities with different levels of resources?

In chapter 3, I explore whether and how different predation strategies can emerge and coexist

together, and what is the impact on food-web structure and species diversity. Predation interactions determine foodweb structure and the predator-prey interactions with the highest PPMRs act to stabilise the community and act as buffer against perturbations to maintain ecosystem functioning (Brose et al., 2019). Therefore it is vital to identify how different predation strategies emerge to preserve them. However, there is a considerable degree of variation in observed PPMRs, meaning that predator traits are not enough to explain PPMRs in marine ecosystems (Brose et al., 2019). I hypothesise that productivity also influences the evolution of PPMRs. Using the model, we focus on sized-based interactions, incorporating eco-evolutionary dynamics to track (i) the emergence of different PPMR values in a multi-species ecosystem, and (ii) their dependence on resource availability.

Question 3 How do species' thermal performance traits evolve under stable versus highly variable climates?

In chapter 4, I use the model to explore evolutionary changes in fish thermal performance in the context of ocean warming. The impact of global warming on natural systems is driving rapid ecological and evolutionary change. Fish species demonstrate variable ranges of thermal performance, and cover the spectrum from temperature specialists (i.e. tropical species) to temperature generalists (i.e. temperate species). It is unclear which of these two strategies are beneficial under different projected warming scenarios and how species interactions might affect the emergence of thermal performance traits. In the model, fish thermotolerance is categorised as two traits (i.e. optimum temperature and temperature generalist/specialist). I explore evolutionary changes in fish thermal performance (thermal optimum and range), and changes in the community structure in response to past and projected sea surface temperatures for southeast Australia. This work demonstrates that rapid adaptation can buffer species under harsh environmental changes, but only for a few decades.

In Chapter 5, I conclude with a general discussion about the key insights that have emerged from this thesis and I integrate the model into a new R package, to provide a resource for tackling future research questions about the evolutionary ecology and biodiversity of rapidly changing ecosystems.

Note: I use the word "I" in chapters 1 and 5 but the word "we" in chapters 2 through 4 which are collaborative works.

The main body of the thesis (Chapters 2-4) is presented as three stand-alone papers developed for publication. Accordingly, it is inevitable that there is overlap in the Introduction and, to a lesser extent, Discussion sections of these chapters.

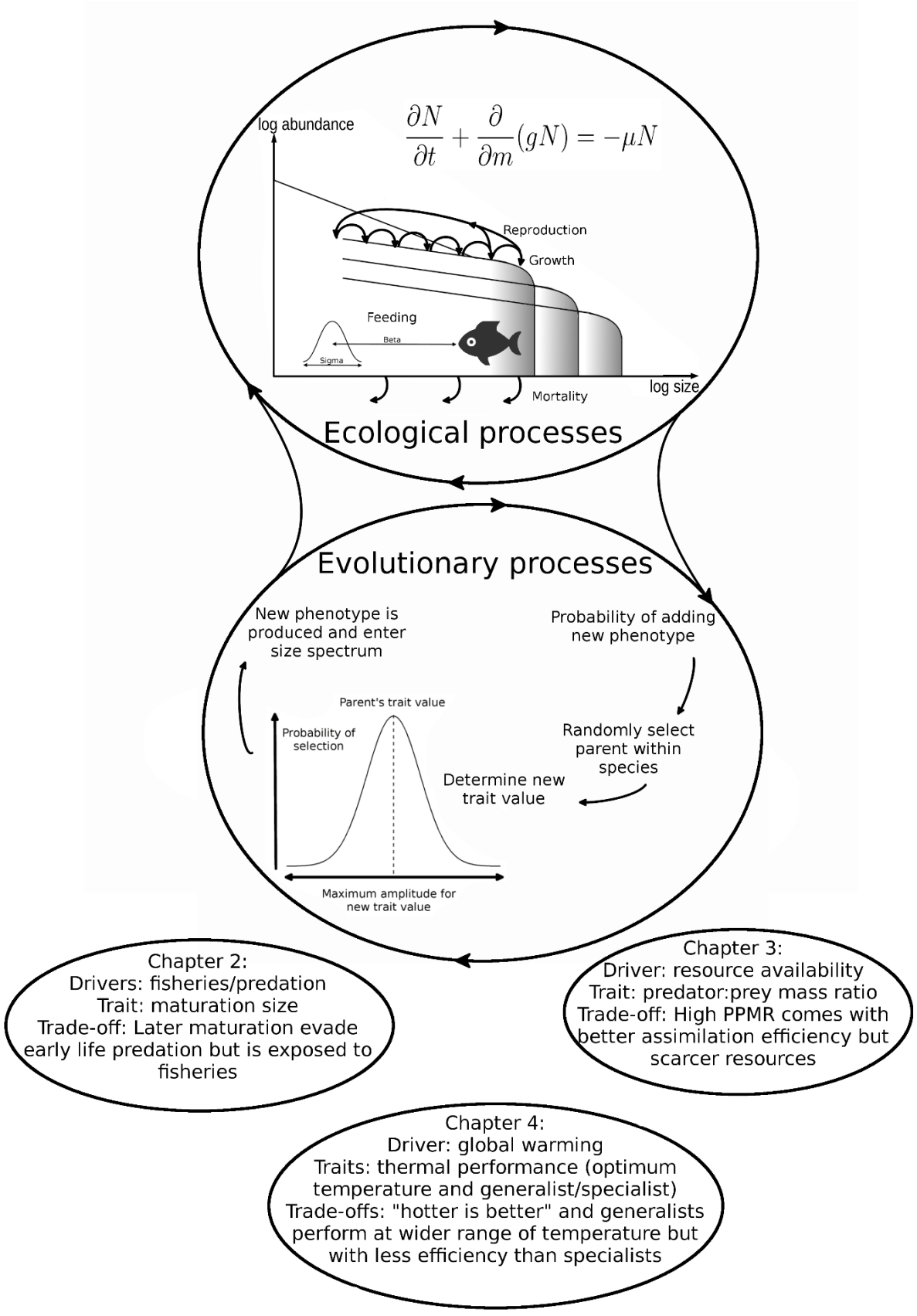

FIGURE 1.2: Conceptual structure of the model and thesis. The top cycle represents the ecological processes modelled by Mizer. The cycle below is my thesis addition to Mizer through evolutionary processes. The three bubbles at the bottom summarise the three data chapters with their drivers, traits studied and trade-offs.

Chapter 2

Interacting forces of predation and fishing affect species' maturation size

2.1 Summary

1. Fishing is a strong selective force and is supposed to select for earlier maturation at smaller body size. However, the extent to which fishing-induced evolution is shaping ecosystems remains debated. This is in part because it is challenging to disentangle fishing from other selective forces (e.g. size-structured predation and cannibalism) in complex ecosystems undergoing rapid change.

2. Changes in maturation size from fishing and predation have previously been explored with multi-species physiologically structured models but assumed separation of ecological and evolutionary timescales. To assess the eco-evolutionary impact of fishing and predation at the same timescale, we developed a stochastic physiologically size-structured food web model, where new phenotypes are introduced randomly through time enabling dynamic simulation of species' relative maturation sizes under different types of selection pressures.

3. Using the model, we carried out a fully factorial *in silico* experiment to assess how maturation size would change in the absence and presence of both fishing and predation (including cannibalism). We carried out ten replicate stochastic simulations exposed to all combinations of fishing and predation in a model community of nine interacting fish

species ranging in their maximum sizes from $10g$ to $100kg$. We visualised and statistically analysed the results using linear models.

4. The effects of fishing on maturation size depended on whether or not predation was enabled and differed substantially across species. Fishing consistently reduced the maturation sizes of two largest species whether or not predation was enabled and this decrease was seen even at low fishing intensities ($F = 0.2yr^{-1}$). In contrast, the maturation sizes of the three smallest species evolved to become smaller through time but this happened regardless of the levels of predation or fishing. For the four medium-size species, the effect of fishing was highly variable with more species showing significant and larger fishing effects in the presence of predation.

5. Ultimately our results suggest that the interactive effects of predation and fishing can have marked effects on species' maturation sizes, but that, at least for the largest species, predation does not counterbalance the evolutionary effect of fishing. Our model also produced relative maturation sizes that are broadly consistent with empirical estimates for many fish species.

Keywords

body size, coexistence, evolution, fisheries, food webs, multi-species size spectrum model

2.2 Introduction

The last century has been marked by a rapid decline in the health of many ecosystems due to exploitation, invasive species, climate change, pollution and eutrophication (Smith, 2003; Halpern et al., 2008). These drivers represent strong selective pressures, and rapid evolutionary responses have been documented in many organisms and ecosystems (Palumbi, 2001; Darimont et al., 2009; Sullivan et al., 2017). In marine ecosystems one of the major ecological and evolutionary forces is fishing (Jorgensen et al., 2007; Audzijonyte et al., 2016; Fugère and Hendry, 2018). Fishing can alter body size structure, size specific mortality, optimal life

histories, and lead to evolution towards earlier maturation, smaller adult body sizes, and altered behaviour (Conover and Munch, 2002; Audzijonyte et al., 2013a; Therkildsen et al., 2013). Evolution of maturation and body size in response to size selective fishing has been demonstrated in experimental studies (Conover and Munch, 2002; Uusi-Heikkilä et al., 2015) and single species models (de Roos et al., 2006; Enberg et al., 2009). However, outcomes of experimental studies cannot be easily extrapolated to real ecosystems, because it is unclear how ecological and evolutionary feedbacks through species interactions might modify selection pressures imposed by fishing (Kuparinen and Merilä, 2007).

Life-history theory makes it clear that increased adult mortality will select for earlier maturation (Charnov et al., 2013). Although wild fish stocks around the world have been observed to follow a trend towards earlier maturation and smaller maximum body size (Olsen et al., 2005; Audzijonyte et al., 2013b, 2016), debate remains as to whether this can be explained by fishing induced evolution (FIE) (van Rijn et al., 2017). Multiple drivers can affect maturation and body size and similar changes are also observed and expected in response to increased water temperatures (Blanchard et al., 2005; Baudron et al., 2014; Audzijonyte et al., 2016). The combined effect of these pressures on trait evolution is not straightforward to predict. For example, high predation can also drive evolution to earlier maturation in wild populations (Reznick et al., 1997, 2008) and predation on small individuals may override evolutionary selection from low fishing intensity, and even drive an increase in maturation size (Edeline et al., 2007). Furthermore, increased and decreased maturation size were both observed in a single predator-single prey model, that included competition and cannibalism, when increased mortality was applied to small individuals; this is because change in maturation size proved to be dependent on how mortality changed with body size (Claessen et al., 2002; Gårdmark et al., 2003). As fishing pressure increased in many intensively harvested areas, predation mortality has declined substantially, due to large changes in the biomasses and size structure of top predators (Fisher et al., 2010), leading to large effects on the abundance of smaller species (e.g. Shackell et al. 2010). These studies suggest that a universal decrease in maturation size in response to fishing may be unlikely in complex multi-species ecosystems, where multiple

species are fished and interact through predation and competition. Understanding and predicting FIE in a multispecies context therefore requires better representation of the potential interactions between fishing and other ecological selection forces.

The debate on the universality of FIE has important implications for precautionary fisheries management. If evolutionary responses to fishing are unpredictable and varied, it is unrealistic to expect its inclusion in forecasts of stock productivity. It would also mean that the widespread trends towards earlier maturation in many harvested stocks could be caused by factors other than, or in addition to, fishing (e.g. climate change) (see Audzijonyte et al. 2016; van Rijn et al. 2017). On the other hand, if under most conditions fishing does select for earlier maturation at smaller body size in multi-species systems, fisheries managers should be encouraged to account for such trends in their management plans. To address the role of species interactions and eco-evolutionary feedbacks on the evolution of fish maturation size under fishing we used a multi-species size spectrum model with temporal adaptive evolution of maturation size. The need for this kind of model is well recognised (e.g. Fraser 2013), yet most marine ecosystem and multi-species models do not include selection-driven (as opposed to random) evolutionary changes (Belgrano and Fowler, 2013).

Individual body size is widely accepted as one of the most important functional traits, especially in marine ecosystems, and size spectrum food web models have been successfully applied to study changes in individual body size distributions of communities and ecosystems (Blanchard et al., 2017a). Size spectrum models can resolve the detailed demography of species by characterizing maturation and asymptotic sizes, as well as enabling given sizes of particular species to interact with other sizes and species through predation (including cannibalism) and competition (Hartvig and Andersen, 2013).

The inclusion of maturation size in size spectrum models makes them particularly useful for addressing questions related to adaptive maturation responses to fishing. Indeed these kinds of models have previously been coupled with adaptive dynamics models to explore the long-term effects of different selective forces on maturation sizes. For example, interference competition, in combination with predation but without fishing, has been shown to influence the distribution and

diversity of maturation sizes at equilibrium in a modelled community size spectrum (Zhang et al., 2015). Fisheries-induced evolution has also been studied using a similar modelling framework. Law and Plank (2018) used a two species size spectrum model to explore the effects of different size-structured harvesting strategies on maturation size changes, emphasising the importance of including both intra- and inter-specific predation. They also suggested that to usefully inform contemporary fisheries management, closer examination of the intricacies of multi-species systems at shorter time-scales would be warranted (Law and Plank, 2018). The adaptive dynamics approach used in these and other models (Dieckmann and Law, 1996; Gårdmark et al., 2003) assumes a separation of ecological and evolutionary time scales, with fast ecological dynamics influencing selection acting on species and size classes and the introduction of new species occurring at equilibrium. However, evidence of rapid evolution and eco-evolutionary feedbacks is well recognised and ubiquitous (Ellner, 2013; Matthews et al., 2016; Beckerman et al., 2016), meaning that ecology and evolution happens on the same time scales.

Inspired by the above adaptive dynamics studies, we develop a model that allows us to investigate the consequences of traits adapting and changing through time, but with the introduction of new phenotypes occurring at the same timescale as the ecological processes of feeding, growth, mortality and reproduction. We have extended the physiologically structured multi-species size spectrum modelling approach to explore temporal eco-evolutionary dynamics of maturation size and its response to fishing. With this model we tackle the central questions regarding FIE, namely whether and how ecological interactions (e.g. intra- and inter-specific predation) affect fisheries-induced selection pressures on maturation size (Kuparinen and Merilä, 2007; Edeline et al., 2007; Carlson et al., 2007). We ask three main questions. Does, in accordance with single species predictions, FIE lead to universally declining maturation size? How does the interaction of fishing versus predation (and cannibalism) pressure affect the emergent maturation size for species of different asymptotic sizes and hence different trophic roles? What is the minimum fishing intensity necessary to trigger FIE responses in maturation size?

We expect that strong size-selective fishing will select for earlier maturation size. However, we expect that predation (which for our purposes includes cannibalism) will also lead to changes

in maturation size, but that the direction of these changes is harder to predict because predatory interactions are more complex than the pressures arising from size-selective fisheries. We explore whether predation can counterbalance the evolutionary pressure from fishing in species at different trophic levels and assess at what level of intensity fishing becomes the overpowering selective force.

2.3 Methods

In this study we explore the eco-evolutionary feedbacks between fishing, community dynamics and dynamic temporal changes (evolution) in maturation size. To model community dynamics we used a modified version of the trait–based size spectrum model (Andersen and Pedersen, 2010; Hartvig et al., 2011) implemented in the R package "mizer" (Scott et al. 2014; which also provides further documentation). Our modifications to "mizer" include the introduction of eco-evolutionary dynamics (the code is available on https://github.com/baldrech/MizerEvo). The modelling approach has two components: 1) an ecological component, which defines intra- and inter-specific interactions that act as selective forces influencing survival and community dynamics (i.e. as in the basic "mizer" package), and 2) an evolutionary component that generates random new trait values (i.e. maturation size), which are introduced in the community at each time step. A conceptual model illustration is shown in Fig.2.1 and below we describe the key components of the model with equations and parameters provided in Tables 2.1,2.2 and 2.3 (for further details on the assumptions in the "mizer" package see https://sizespectrum.org/mizer/).

Ecological component

Size spectrum models are physiologically structured models that track the density of individuals at size through time (Andersen, 2019). The trait-based approach means that the model has several "species" or size spectra, which differ only in their asymptotic and maturation size (maturation size is assumed to be a fraction of asymptotic size). This modelling approach has the desired combination of model simplicity (only one set of physiological parameters required), but still allows for multiple species with variable maturation sizes.

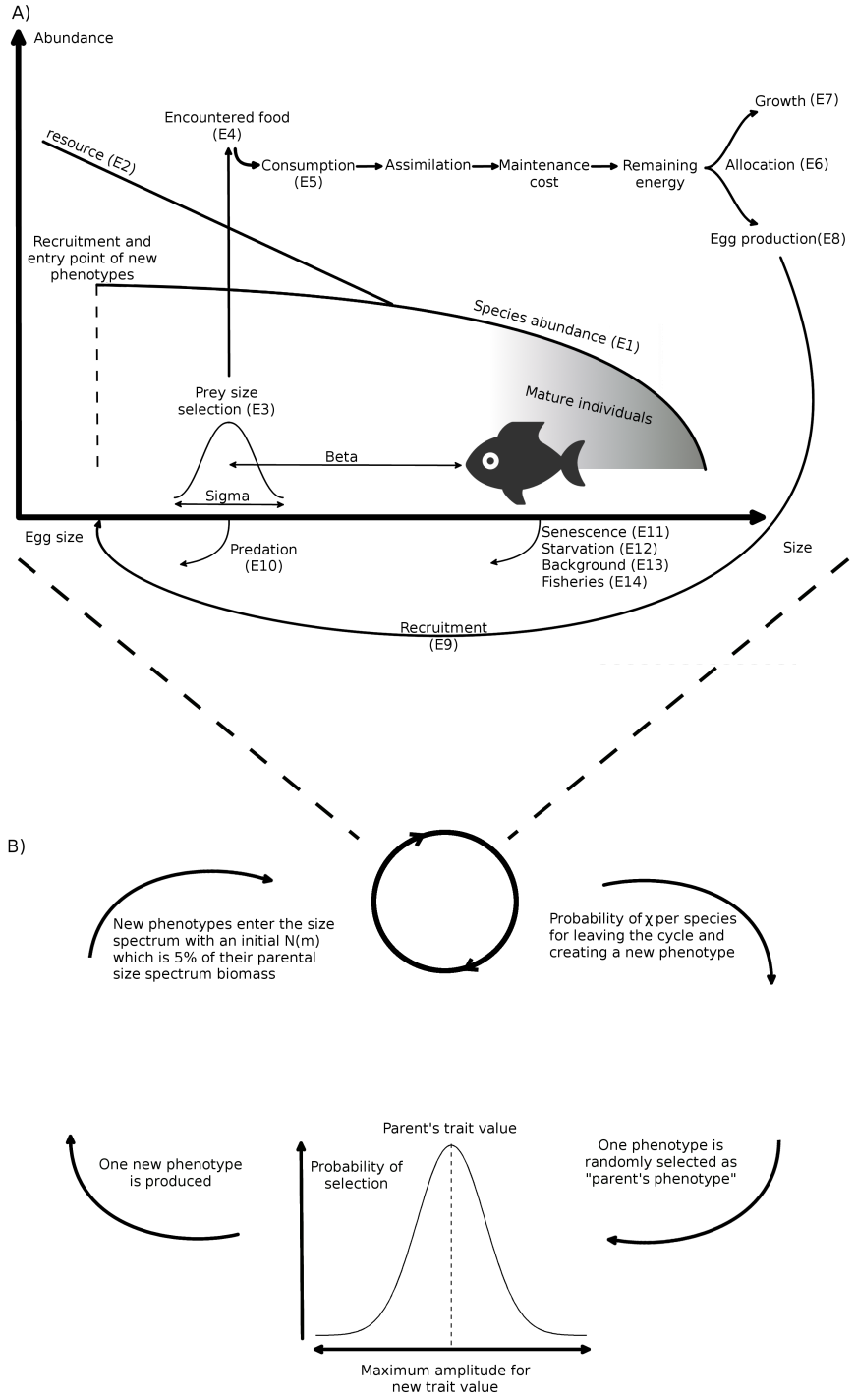

FIGURE 2.1: Schematic representation of key model components. A) shows the energy pathways occurring in the model through the different equations found in Table 2.2. E1, E2 and E9 govern the abundance of the different components. E3 to E5 are used for energy intake which is then divided between growth E6 and reproduction (E8) depending on the maturation state (E7). Mortalities are described by equations E10 to E14. B) shows the evolutionary processes built around the ecological model.

Growth, maturation and reproduction are all food-dependent, and driven by the process of size-dependent predation, and the model therefore includes emergent intra- and inter-specific competition. This means that the evolution in response to fishing and predation is studied against a backdrop of underlying ecological competition. Feeding, growth, mortality and reproduction occur at every time step. The flux of individuals between size bins depends on growth (inflow from smaller size bin, outflow to larger size bin) and mortality. The population dynamics of each species is then obtained by solving the conservation equation (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$$

where m is the species mass and individual growth $g(m)$ and mortality $\mu(m)$ are determined by predation on/from other individuals, and a background resource spectrum modelled using a semi-chemostat growth assumption (Table 2.2, E2).

Food consumption

In this model all individuals are simultaneously predators and prey, where no distinction is made between inter-specific predation and cannibalism. The available food comes from all of the fish species and a background resource size spectra, which here is assumed to extend from 10^{-10} to $1g$ (bacteria to zooplankton) (Table 2.3, with the same regeneration rates as in Hartvig et al. 2011). All species begin life at the same size ($0.001g$) and compete for food in the resource size spectrum. As they grow larger the extent to which they feed on themselves and each other is dictated by a species interaction matrix and size-based feeding kernel. A species by species interaction matrix scales the proportion of available biomass of each prey species to each predator species, with the diagonal setting the intensity of cannibalism. Here we used two contrasting symmetric interaction matrices with all values set to either 0.5 or 0, depending on whether predatory interactions were included or not (see below). We chose 0.5 to define the predatory interactions, assuming that prey biomass is never completely available to predators at

any given time, due to spatial or temporal separation and predator avoidance behaviour. When the interaction matrix is set to 0 all sizes and species compete for food in the resource size spectrum. Encountered food is the product of the volumetric search rate that scales with body size and the availability of food within the size spectrum (Hartvig et al., 2011).

Whether or not encountered prey are eaten is determined by a size-dependent feeding kernel with the preferred predator:prey mass ratio β and width of the feeding kernel σ (Table 2.3), and is described by a log-normal selection model:

$$\phi(m_p, m) = exp\left[\frac{-(ln(m/(\beta m_p)))^2}{2\sigma^2}\right]$$

where m_p is prey mass and m the predator mass.

Once the available size range has been determined, the realised food consumption is modelled through a standard Holling type II functional response, determined by the search rate and maximum intake rate, resulting in the emergent feeding (satiation) level (Table 2.2, E4 - E5).

Growth

The consumed food is assimilated with an efficiency α and the resultant energy is divided between metabolism and growth (Table 2.2, E6), with the latter further divided between somatic growth and reproduction (Table 2.2, E7) depending on the maturation status. Resource allocation between growth and reproduction follows a logistic curve, where half of the growth resources are allocated to reproduction at maturation size, making fecundity scale with body size. We have modified E7 from Hartvig and Andersen (2013) and the 'mizer' default equation by changing the scaling parameter (u, table 2.3) of energy allocation to reproduction from 10 to 7 to allow for a more prolonged period between minimum and maximum investment in reproduction.

Reproduction

New recruits enter the smallest size class at every time step, i.e. the model assumes continuous reproduction (Table 2.2, E8 and Table 2.3). Recruitment is determined using the Beverton-Holt type stock recruitment relationship (Andersen and Pedersen, 2010), defined by equation E9 (Table 2.2) and the maximum flux recruitment parameter R_{max} (Table 2.1) (see below for further details on recruitment in the evolutionary model). An upper limit on the recruitment flux (R_{max}) is used to impose additional density-dependence otherwise not captured by the processes in the ecological model, but that are recognised to be important in marine fish populations (which also leads to an emergent stock-recruitment relationship; e.g. Andersen et al. 2016b).

Mortality

In addition to the emergent predation mortality, other sources of mortality include senescence mortality (Table 2.2, introducing survival cost of reproduction, e.g. Kuparinen et al. (2012), E11), starvation mortality (Table 2.2, E12), a constant background mortality where larger species are assumed to have lower background mortality (Hartvig et al., 2011) (Table 2.2, E13), and fishing mortality (Table 2.2, E14).

Evolutionary Component

In this study we explore evolutionary changes in a single trait - maturation size. This was modelled through the η parameter, which defines the fraction of the theoretical asymptotic size at which 50% of an individual's net energy is allocated to reproduction (Table 2.3). We chose to modify η rather than asymptotic size (as in Zhang et al. 2015) to ensure that dynamic change in η only affects the resource allocation and the emergent growth, but not the background mortality which depends on theoretical asymptotic size (Table 2.2, E13). Changes in η through time were modelled similarly to the unstructured eco-evolutionary food web model of Allhoff et al. (2015) by introducing new size spectra ("phenotypes") characterized by new trait combinations. In contrast to Allhoff et al. (2015), however, who ran their simulation to equilibrium before adding new phenotypes (mutations) we allowed for a possibility of new phenotypes to appear at each time step, assuming a constant influx of new mutations. Our approach assumes no interbreeding

among phenotypes (new genetic variation is only generated via the mutation process), because each phenotype produces offspring identical to itself and no intermediate trait values among phenotypes emerge. This approach is also similar to that used in adaptive dynamics (Dieckmann and Law, 1996). As the simulations ran, each species generally had 10-50 phenotypes (Fig.S.1, appendix B, showing the number of phenotypes per species through time), turning over their abundances through time in response to the selection forces at play. Our approach approximates temporal dynamics of η in response to selection by tracking each phenotype through time and computing the changing mean and variance of η for each species.

These new phenotypes were generated by randomly selecting an already existing phenotype (i.e. set of parameter values) within a species to represent a "parent". At each time step there is an equal probability that each species will generate a new phenotype. The new phenotype is a copy of its parent except for the maturation size for which values are randomly drawn from a normal distribution ranging from -20% to 20% of the parent's trait value (Fig. 2.1). The initial abundance of the new phenotype was assumed to be 5% of the parent's biomass, which is subtracted from the parent's biomass. This means that phenotypes of less abundant parents have low initial abundance and lower chance to become established in a population, to ensure that the realized rate of evolution depends on the population size. Following their entrance into the ecosystem at egg size, the phenotypes compete for food and are predated upon, and hence change in abundance. The extinction threshold was set at $\Omega = 10^{-30} ind.m^{-3}$ (Hartvig et al., 2011) and all phenotypes below this density were removed. The probability of new phenotype appearance χ was set to 0.001 per time-step and the initial η vales were assumed to be 0.25 for all species (Hartvig and Andersen, 2013). This combination of parameters produced an expected evolutionary rate similar to that observed in populations with high fisheries intensity (Audzijonyte et al. 2013a, see Discussion). To ensure robustness of these parameters for our findings, we explored the sensitivity of different values of χ and initial η along with other key parameters (Appendix A).

Balancing extinction and coexistence through food limitation

We focus on the eco-evolutionary interactions between predation and fishing against the backdrop

of food limited conditions, that includes inter- and intra-specific competition for resources. Food limitation is needed to enable some competition, extinction of less fit phenotypes, and temporal change in maturation size. The application of a maximum recruitment R_{max} assumes strong density dependence early in life; lower R_{max} leads to lower recruitment and reduces competition for a given resource density, while high R_{max} leads to competitive exclusion by one or a few species (Andersen et al., 2016b). Because we are focussed on modelling evolutionary changes against the backdrop of food limitation, the initial R_{max} values were set for each species assuming the default values provided in the trait-based model of 'mizer' (see also Andersen 2019) and predation/resource parameters were calibrated (σ, κ and r_0, Table 2.3) to ensure a balance of coexistence and food limitation (feeding levels between 0.12 and 0.7) (Table 2.1).

The phenotypes behave like separate species in that their size spectra are tracked independently and they compete with each other. However, all phenotypes in one species are affected by the same R_{max}. This means that during reproduction, all offspring are pooled within each species, one R_{max} applied to all of them to calculate the new offspring numbers, and these are then distributed among phenotypes in proportion to their spawn output (i.e., a phenotype with a high spawn output will have more recruits with its traits than a phenotype with a low spawn output). Thus, abundant phenotypes are not disproportionally affected by R_{max}, which would be the case if it was applied to each phenotype separately.

Fitness calculations

As phenotypes are constantly being introduced and becoming extinct, the resulting fitness landscape and eco-evolutionary dynamics are ever-changing. We calculate fitness landscapes at several time intervals to explore the selection pressures on phenotypes through time.

We track the cohort survival and fecundity through time for 50 years (t_{max}), using a modified version of $R0$ (lifetime reproductive output) as a proxy for fitness:

$$fitness = \frac{\int_{t_0}^{t_{max}} R_{max,i} \frac{R_{p,i}}{R_{p,i}+R_{max,i}} dt}{N_{p,i}(m_1, t_0)}$$

TABLE 2.1: Initial maturation, asymptotic size and R_{max} of the species.

Species	Maturation size (g)	Asymptotic size (g)	R_{max}
1	2.5	10	0.49208
2	8	32	0.19854
3	25	100	0.08011
4	79	316	0.03232
5	250	1000	0.01304
6	790	3162	0.00526
7	2500	10000	0.00212
8	7905	31622	0.00085
9	25000	100000	0.00034

where $R_{p,i}$ is the energy allocated to reproduction (E8) by phenotype p of species i, $R_{max,i}$ is the maximum recruitment value for species i and $N_{p,i}(m_1, t_0)$ is the initial numbers of phenotype p and species i in the cohort of interest. This measure is similar to "eggs per recruit" (Andersen, 2019). We used this fitness calculation to construct snapshots of fitness gradients (in relation to maturation size) for all species' phenotypes across all simulations to assess whether modelled directional changes are consistent with these gradients. Because different species have different R_{max} values, the fitness cannot be quantitatively compared across species, but they are comparable across phenotypes within a species where the same R_{max} value applies.

Simulation design

To assess how predation affects evolution of species' maturation size under fishing, we conducted simulations using four different model scenarios – with and without fishing and with and without predatory interactions (interaction matrix set to 0.5 or 0 respectively). In all simulations we used a model composed of 9 species with asymptotic sizes equally spread on a logarithmic scale between 10 to $10^5 g$. The initial abundance of each species was determined based on the equilibrium conditions (Andersen and Beyer, 2006), which uses feeding and carrying capacity parameters to estimate biomass at equilibrium. When predatory interactions are disabled all species only feed on the background resource spectrum, but they still compete for food.

Fishing was imposed through a knife-edge selectivity function, where all fish at or above the selected size were subjected to an instantaneous fishing mortality rate. For simplicity and to

minimize the number of alternative fishing scenarios, the selected size for all species is set at 0.25 of asymptotic size (i.e. at the initial maturation size). For the main set of scenarios, we applied the instantaneous fishing mortality $F = 0.8yr^{-1}$, as this was high enough to trigger ecological and evolutionary responses, but sufficiently low to avoid extinctions, and represents fishing pressure historically applied to many fish stocks (RAM Legacy Stock Assessment Database, 2020). To assess the sensitivity of model outcomes to fishing intensity we also explored the results with fishing mortality ranging from 0.1 to 1.0 per year.

Since the eco-evolutionary dynamics and fitness values change throughout the simulations as new phenotypes appear, the model is not necessarily expected to reach equilibrium conditions. To account for stochasticity of the eco-evolutionary dynamics, each scenario (parameter combination) was repeated 10 times. To test whether 10 stochastic realisations were enough to capture trends, we also ran all predation-enabled scenarios with 50 replicates but found no substantial difference in trait changes and variances (See Fig.S.7 and S.8 in Appendix A).

The simulations were run for 3000 years without fishing to allow the ecosystem to build up multiple phenotypes per species, establish evolutionary trends in the absence of fishing and for the influence of initial conditions to dissipate. After 3000 years, the full simulation state of each stochastic run was saved and used to initiate two additional 3000 years of simulations, with and without fishing imposed. The effects of fishing on the evolutionary dynamics were assessed by comparing dynamics and final states in simulations with and without fishing.

The sensitivity of the model outcomes to the parameter values was assessed across a range of: fishing mortalities (0.1 to 1); the initial trait value η (Fig.S.1); the standard deviation between parent and new trait (Fig.S.2); new phenotype appearance rate χ (Fig.S.3); the initial phenotype abundance (Fig.S.4); width of the feeding kernel σ (Fig.S.5); and preferred predator-prey mass ratio β (Fig.S.6).

Analyses of simulation outputs

We assessed the modelled communities by exploring phenotypes' abundance history (i.e., phenotype biomass time series including when they appear and go extinct) and evolutionary trends of

each species' average relative maturation size η. This was calculated as the abundance weighted mean trait value across all phenotypes for each species in each simulation through time. Since the simulations were conducted as a factorial design (predation x fisheries) we tested whether final values of η (after 6000 years) depended on the interaction of Species*Predation*Fishing using a three-way Model 1 (fixed effects) ANOVA, where Predation (0 or 1), Fishing (0 or 1) indicate presence or absence of predation and Species is the species number,with $n = 10$ replicate simulations. To ensure among-group homogeneity of variance in residuals we log-transformed η (after transformation the homogeneity was achieved).

All three terms and their interactions were evaluated using F-tests and model comparisons were carried out using delta AIC tests. While we report p-values, the purpose of these models was to evaluate and interpret the nature of the interactions in the model. Statistics were done using R version 4.0.0 (R Core Team, 2020), the 'effects' (v4.1-4; Fox et al., 2019) and the 'emmeans' (v1.4.7; Lenth et al., 2020) packages. The lower and upper 95% confidence intervals for all model predicted effects were calculated using the allEffects function in the R package 'effects'.

To assess whether the final values of maturation size (η) were compatible with empirical observations, we compared our results with empirical estimates for wild fish stocks (Rijnsdorp et al., 1992; Reznick et al., 1997; Jennings et al., 1998; Conover and Munch, 2002; Goodwin et al., 2006; Ulloa et al., 2011; Olsson and Gislason, 2016).

2.4 Results

Maturation size trajectories

During the initial 3000 years of simulations without fishing, the presence of inter- and intraspecific predation had large effects on the evolution of maturation sizes (Fig.2.2). In simulations without predation the relative size at maturation decreased substantially ($40-90\%$) in all but the largest two species (Fig.2.2b, before the dashed line). In contrast, when predation was enabled the evolution of maturation size diverged across the three size groups, where the smallest three species evolved towards smaller maturation (decrease by $45-60\%$), the middle sizes species

towards larger maturation size (increase by 50 – 150%), and in the largest three species the trait evolved slightly in either direction (Fig.2.2d, before the dashed line). After the initial 3000 years, the trend of evolution in scenarios without fishing generally continued in the same direction at a slower rate or stabilised for the remaining 3000 years (difference between the dashed line and solid line in Fig.2.2b and d).

After the introduction of fishing at year 3000, the biomass of many species quickly reached a lower state (Fig.2.2a-c dashed lines), but then recovered in some species as they evolved to adapt to new mortality regimes. In all species and scenarios, fishing led to either decreasing or static maturation size, the latter mostly occurring in cases where maturation size has already evolved to be less than 50% the starting value (except species 5 with predation, Fig.2.2d). For the entire ecosystem, the decline in maturation size due to fishing was stronger when predatory interactions were enabled compared to simulations without predation (strong decrease in maturation size for 5 out of 9 versus 2 out of 9 species in the community, Fig.2.2b-d), suggesting that fishing had a large effect on the ecosystem with predation. Our statistical analyses of the model simulations showed that the effect of fishing (red dots in Fig.2.3) reduced maturation size in medium and large species. All terms of the model were significant (Table S.2) and there was a significant three-way interaction among species, predation and fishing (ANOVA: $F = 2.6$, $df = 8.324$, $p = 0.009$). The differences between maturation size between fished and unfished simulations clearly depended on the species and whether or not predation was enabled. Significantly lower maturation sizes in the presence of fishing were found for species 4, 8, and 9 without predation (pairwise comparison tests, $p < 0.005$) and 4, 6, 7, 8, and 9 with predation (pairwise comparison tests, $p < 0.001$). Across stochastic realisations of simulations, variation in the final maturation size values was generally small for all species when predation was disabled, especially when variation is considered as a proportion of the η (i.e. species with larger η have larger absolute variations in Fig.2.3, but the proportional variation is similar). With predation enabled, variation was small in the three smallest species, and very large in the two medium sized species (species 4 and 5) (Fig.2.3). Sensitivity analyses showed that the observed impacts of fishing were qualitatively similar across a range of tested parameter values (see Appendix A).

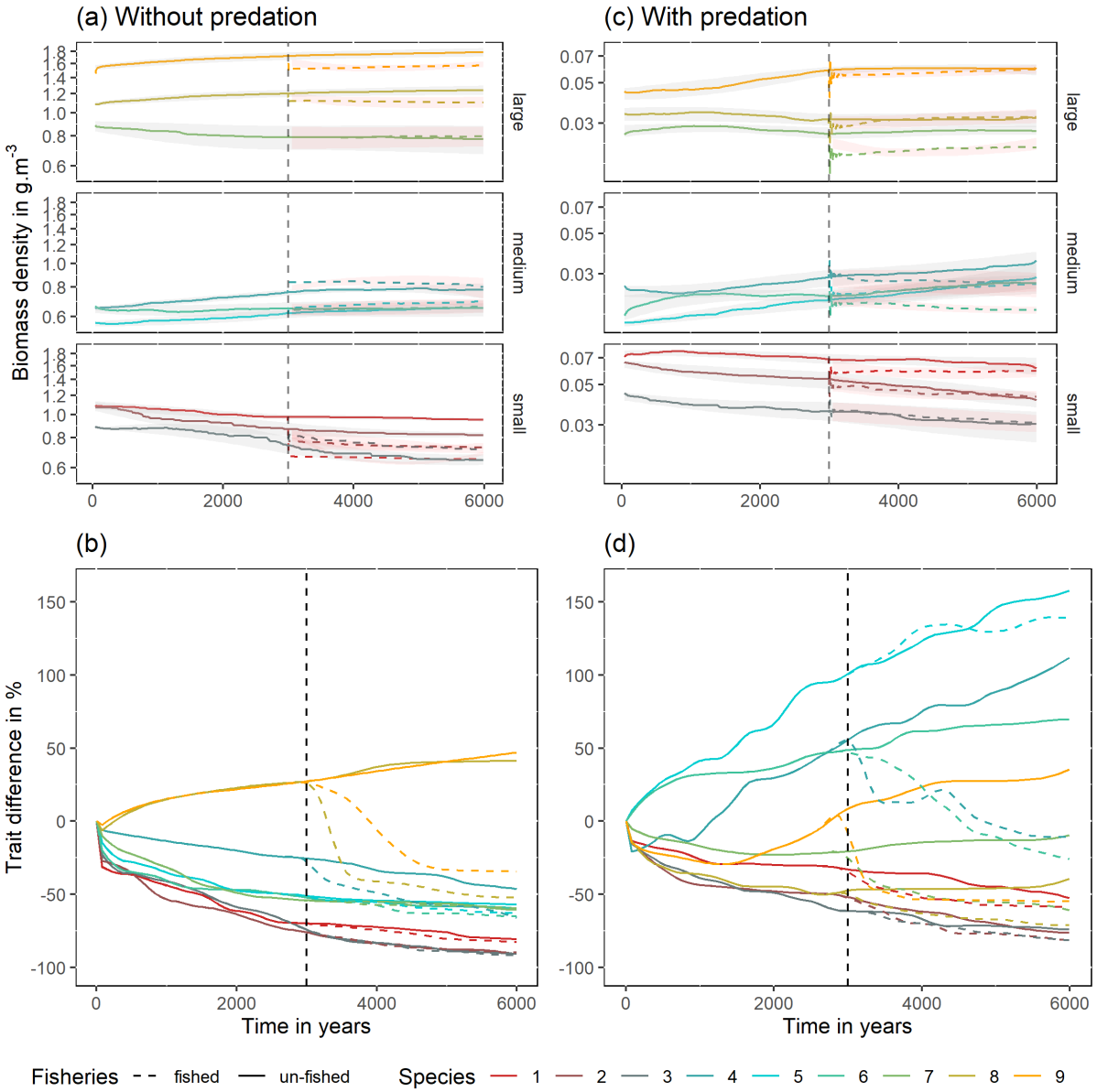

FIGURE 2.2: Biomass and trait variation averaged and smoothed throughout all simulations in scenarios without predation (a-b) and with predation (c-d). (a,c) is the change in species' biomass, the grey shading indicates the standard deviation across simulations. (a,c) is divided in 3 panels (small, medium, large being the species asymptotic size) for more clarity. The vertical line shows the introduction of fishing and from this line, the dashed lines are the biomass when fished, with the red shading showing its standard deviation. (b,d) is the proportional change in weighted mean maturation size for each species relative to its initial value averaged across all stochastic realisations. The vertical line shows the time where fishing is introduced, and the dashed line shows simulations with fisheries.

Maturation size changes in relation to fitness gradients

The species-specific maturation sizes responses to fishing and predation can be in part understood by examining their fitness gradients at a given time (Fig.2.4 shows these at the onset of fishing in

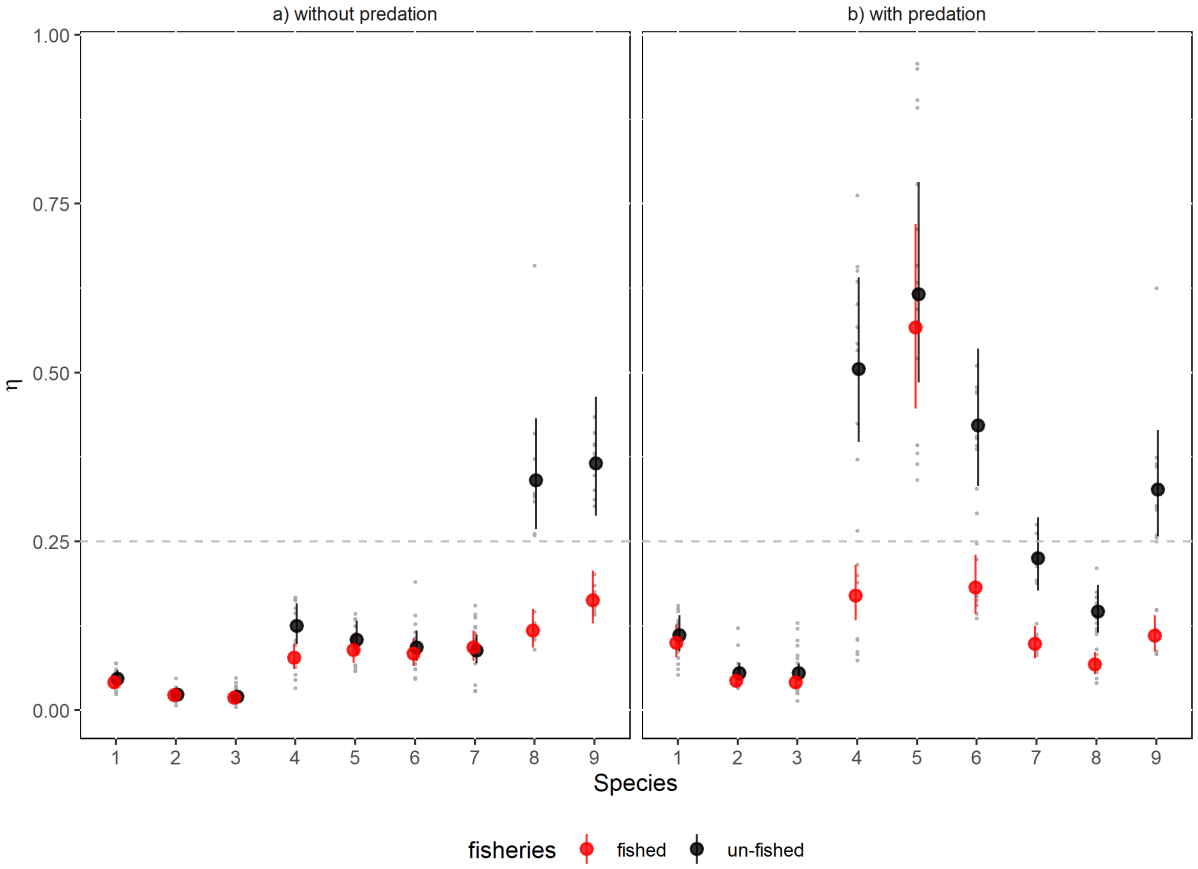

FIGURE 2.3: Final maturation size (relative to each species' asymptotic size) (η) at the end of the simulation (6000 years). Each dot shows the predicted means and 95% confidence intervals from the 3-way ANOVA model for each species, predation and fisheries combination. Data points show weighted average η for each species (across 10-50 phenotypes, see Fig.S.1 for the number of phenotypes per species) where each light grey point is a replicated simulation (10 simulations for each combination of fisheries and predation scenarios). The dashed line indicates the initial relative maturation size value (η).

year 3000, and Fig.S.9 shows them close to the end of the simulation period). For the smallest species neither predation nor fishing had much effect on the fitness gradient, where phenotypes with smaller maturation sizes had slightly higher fitness values, explaining the observed constant and slow evolution towards smaller maturation size. Introduction of fishing generally did not alter the shape of the fitness gradients for these species (red dots compared to the black dots, Fig.2.4, top three rows). In contrast, the medium-sized species' response to fishing strongly depended on whether or not predation was enabled. When predation was disabled, smaller maturation sizes of medium-sized species had higher fitness (Fig.2.4 centre three rows, left panels), explaining their evolution towards smaller body sizes (Fig.2.3 no predation panel)

whereas the opposite was generally true when predation was enabled (except in species 4, where the fitness gradient was not monotonic and either the smallest or largest maturation sizes had the highest fitness). Introduction of fisheries only steepened the fitness gradients in scenarios without predation (both in year 3000 and year 5500, Fig.S.9), making smaller maturation sizes even better adapted while for scenarios with predation the effect of fishing on fitness landscapes was less defined, with large variation across phenotypes (the difference in fitness gradients was more clear for species 6). This response can explain the large variation in the evolutionary trends across stochastic simulations for species 4 and 5 (Fig.2.2d), suggesting that eco-evolutionary dynamics may be less predictable for the medium-sized species because of the interplay of selection pressures from fishing and predation. Finally, the effect of fishing was especially clear on the fitness gradients of the largest species, where smaller maturation sizes always had higher fitness under fishing, and phenotypes with large maturation sizes were largely absent after 2500 years of fishing (Fig.2.4 and S.9).

Impact of increasing fisheries effort

We explored how changes in the intensity of fishing affected trait evolution, by repeating simulations with predation for ten values of instantaneous fishing mortality rate – from 0 to $1yr^{-1}$. For the largest four species (species 6-9) the only level of fishing mortality that did not lead to strong decrease in maturation size was $0.1yr^{-1}$. Increasing fishing mortality to $0.2yr^{-1}$ caused maturation size to decline. Indeed maturation size stayed relatively stable at this new level for all mortality values above $0.4yr^{-1}$ ($0.7yr^{-1}$ for species 6) (Fig.2.5). For the three smallest species changes in fishing mortality did not have much effect, because their maturation size was close to the smallest possible given the physiological trade-offs assumed in the model (i.e. reproductive output is size dependent, so at least some growth is needed for reproduction to occur) and the computational constraints of the model where the maturation size was reached in just a few time-steps. Finally, two of the medium-sized species (species 4 and 5) had large variance in their maturation sizes. For species 5, where fishing did not significantly reduce the maturation size, increasing fishing effort also did not have a clear effect. For species 4, clear effects of fishing on maturation size were seen only at high fishing mortalities ($F >= 0.8yr^{-1}$).

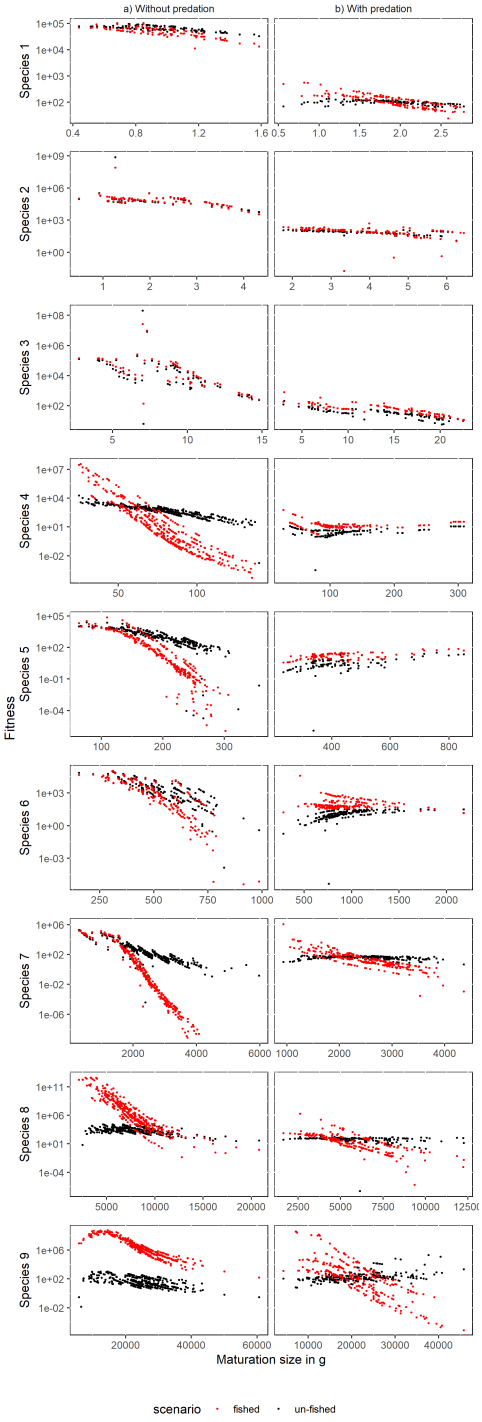

FIGURE 2.4: Species' fitness across simulations. Each dot shows fitness of a phenotype with different maturation size in scenarios with (red) and without (black) fishing across simulations. The figure shows phenotypes in a cohort starting at year 3001 in simulations without (a) and with (b) predation, following the introduction of fisheries. Fitness landscapes in year 5500 were generally similar and shown in Fig.S.9

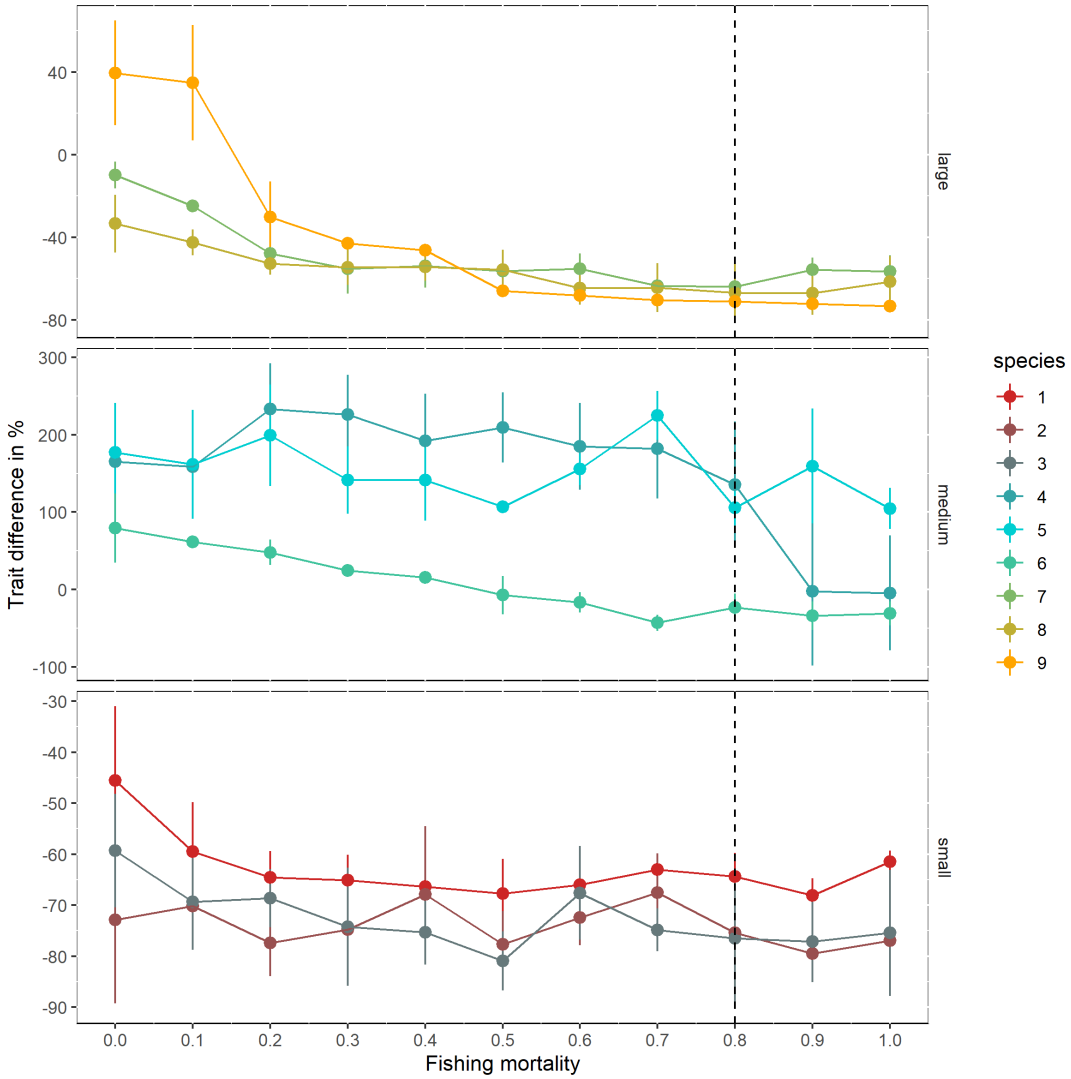

FIGURE 2.5: The effect of the instantaneous fishing mortality rate (yr^{-1}) on changes in maturation size in scenarios with predation. Each line shows the biomass weighted average trait value at the end of the simulation for each species. Error bars show the standard deviation across simulations. The vertical dashed line shows the default parameter values used in the study.

Comparison with empirical patterns

We found that despite divergent evolution of maturation sizes the emergent relationship between the maturation size and maximum body size (at year 6000) generally fell within the range of empirical relationship observed for marine fish across a range of body sizes (Fig.2.6). The overall slope of this relationship remained consistent across simulations with and without fishing.

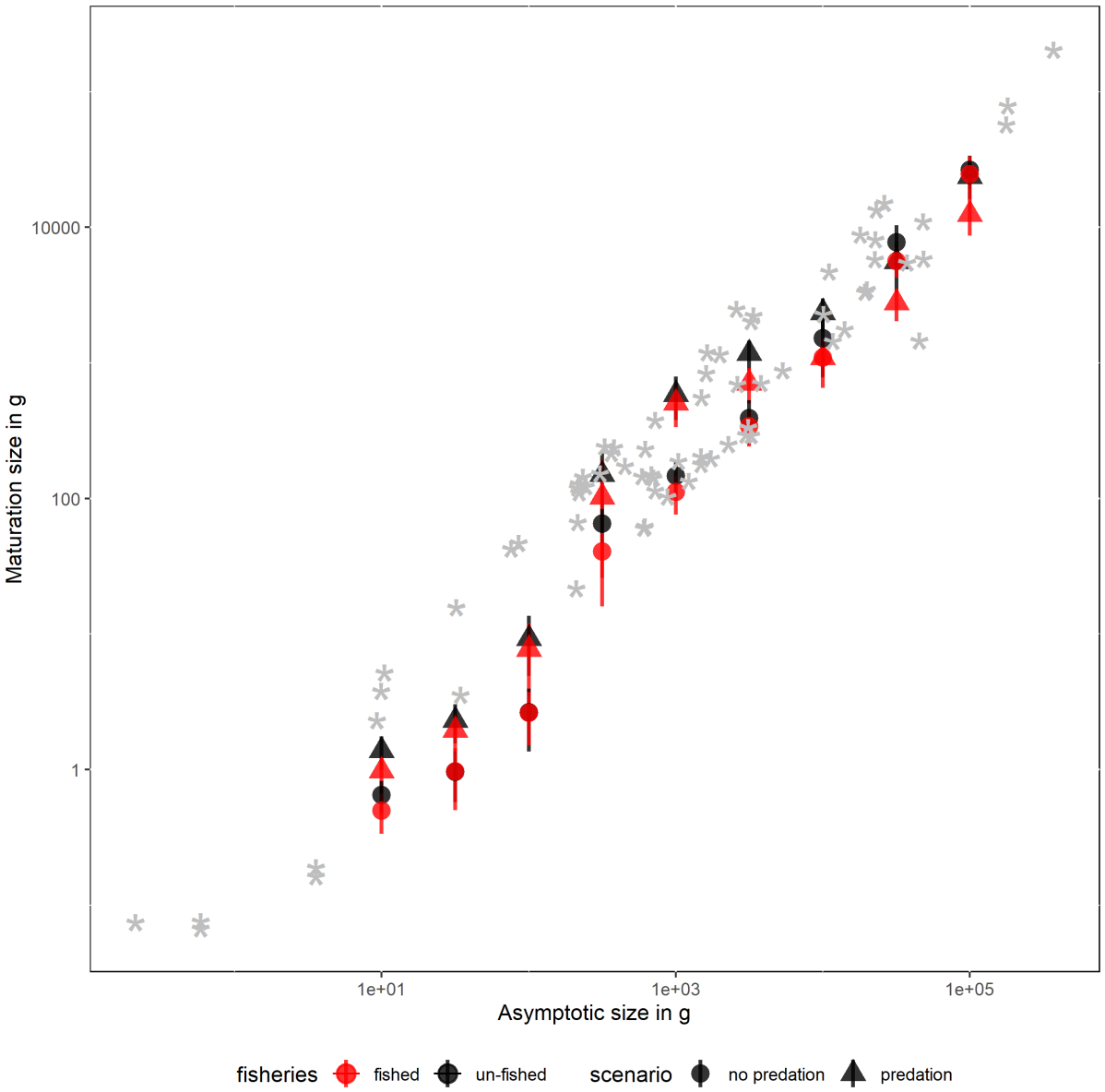

FIGURE 2.6: Modelled and empirical relationship between maturation size and asymptotic size. Modelled estimates of maturation size are from the end of the simulation period (year 6000) with (red) and without (black) fishing and with (triangle) and without (circle) predation. Error bars show the standard deviation across simulations. Silver asterisks are values obtained from empirical studies of fish species for comparison (see table S.3 for data and references).

2.5 Discussion

The eco-evolutionary model presented here aims to tackle the interplay between predatory interactions and size dependent fishing on the evolution of maturation size. The model uses simple rules of size-dependent predation, body size scaling of physiological processes, and introduction of random trait variation. There are four key findings of this study. First, we show

that without any constraints on the direction and limits of maturation size, substantial changes in the evolutionary trends in maturation size emerge, but these changes are broadly consistent with empirically observed patterns. Second, we show that both predation and fishing are strong selective forces, but their effects interact and differ across species of different asymptotic sizes. For the small species, regardless of predation and fishing, species evolved towards smaller maturation sizes. In contrast, predation completely reversed selection gradients in the medium sized species, while fishing generally reversed selection and trait evolution in medium and large species. Third, in agreement with single-species predictions, fisheries generally led to smaller maturation sizes for all but the smallest three species, and its effects were stronger in ecosystems with predation (and cannibalism) enabled. Fourth, for the largest species even low fishing mortality ($0.1 yr^{-1}$) was enough to drive evolutionary change toward smaller maturation size, as predation mortality was considerably lower than fisheries mortality at the largest sizes.

Predation and emergent maturation size

The role of predation on optimal maturation size has been addressed in a range of models, including size spectrum approaches, generally suggesting that maturation sizes diverge to promote species co-existence (de Roos et al., 2006; Hartvig and Andersen, 2013; Allhoff et al., 2015; Zhang et al., 2015). However, these studies used an adaptive dynamics approach and assessed optimal fitness or invasion success of new traits in equilibrium conditions, separating ecological and evolutionary time scales. While the findings of these studies are important, they did not include continuous ecological-evolutionary feedbacks known to shape natural systems (Govaert et al., 2019). Evolutionary feedbacks of species in a multi-species system have previously been suggested to be equally important driver of community response as harvesting (Wood et al., 2018). This is consistent with our findings, which demonstrated that in a number of species the maturation size trajectories varied substantially through time and across stochastic realisations, even when biomass was relatively stable through time. This suggests that the timing and ecological conditions present at the time phenotypes emerged can greatly affect their success, particularly within medium-sized species.

Despite the variation across stochastic realisations and temporal dynamics in trait values, one of the most consistent evolutionary trends seen in our study is the decreasing maturation size of the smallest species in all scenarios, irrespective of predation or fishing. This is illustrated by similar fitness trends across the scenarios (i.e. smallest maturation sizes had higher fitness for small species in all four scenarios of predation and fishing) and could partly be explained by the food limitation at around $10g$ (seen as a drop in feeding level, see Fig.S.2, appendix B). By evolving towards smaller maturation size, species divert fewer resources to growth, can stay longer in size groups between 1 and $10g$, benefit from better feeding conditions, but are not yet exposed to high predation (see panel b in Fig.S.2). Thus, trends in maturation size strongly depend on the resource availability, which is consistent with Hartvig and Andersen (2013), where optimal maturation and asymptotic sizes in a single- or two-species size spectrum models was entirely determined by the resource density. Moreover, Hartvig and Andersen (2013) showed that the system can exist in different stable states depending on whether feeding limitation occurred at an early juvenile stage or around the maturation size (see Claessen and de Roos 2003, for a similar finding in an age-structured model). This means that some combinations of size-specific resource limitation and maturation size are unstable and will select for either smaller or larger maturation size.

The key difference between Hartvig and Andersen (2013) and our study design is that the former explored the evolution of asymptotic size, while always setting the maturation size to be a fixed proportion of the asymptotic size. Yet, asymptotic size also determined background mortality (which can be high in small species) and the final evolutionary drivers (competition, predation or differences in background mortality) were hard to identify. The factorial design of our simulations aimed to tease apart some of these drivers. Also, by specifically allowing for evolution of the η parameter, we allow the maturation size to evolve independently of the asymptotic size without affecting the background mortality. Additionally, we introduced the survival cost of reproduction (small increase in mortality after maturation), which are ubiquitous in nature and have an effect on evolution of maturation size (Kuparinen et al., 2012). In our design the asymptotic size becomes a more theoretical parameter setting the largest possible

body size. In reality, as maturation size, growth rates, and mortality evolve and change through time, many species never reach their asymptotic sizes. Nevertheless, both our and Hartvig and Andersen (2013) study share the same general finding – food limitation at around the maturation size will act as a strong selective force (for small species in our study).

Another notable finding is the evolution of maturation size in medium sized species, where predation reverses the maturation size trends and leads to a rapid increase rather than decrease in maturation size seen in scenarios without predation. Together with large variation in maturation sizes in middle sized species this suggest that alternative maturation strategies might exist for these species, all dependent on the dynamic size specific mortality from predation and fishing. Although we did not study alternative stable states, our findings are consistent with e.g. Gårdmark and Dieckmann (2006) showing that such alternative stable solutions do indeed exist. As in Gårdmark and Dieckmann (2006), an important trade-off in our model is the divestment of resources from growth to reproduction at around the maturation size. Delayed maturation size means that more energy at smaller size is available for growth and individuals will move faster to larger size classes, where they can potentially escape predation. The advantage of earlier or delayed maturation will therefore critically depend on the size at which predation mortality is lowest and feeding levels are highest (see also Pope et al. 1994; Duplisea 2005).

Fishing and emergent maturation size

The response of maturation size to fishing has been studied using a range of size and age-structured single-species models (de Roos et al., 2006; Andersen et al., 2007; Enberg et al., 2009). Generally, these studies show that increased mortality due to fishing selects for earlier or smaller maturation size. For example, for the Baltic Sea cod (*Gadus morhua*) the optimal maturation size was predicted (based on single-species and sized structured deterministic model) to be at least 10 times smaller than currently observed (Andersen et al., 2007). Yet, selection in wild populations is a tug of war among predation, pathogenic, competition, sexual selection and human pressures (Edeline et al., 2007; Carlson et al., 2007; Darimont et al., 2007). For fish in particular, predation is a powerful force, imposing strong selection on size, especially

early in life (Perez and Munch, 2010), but also in adult individuals (Olsen and Moland, 2011). The strength of predation (including cannibalism) can counteract or even reverse evolutionary effects of fishing, such as in Lake Windermere pike *Esox lucius* (Edeline et al., 2007). It is therefore unclear how often and for which species harvest induced selection might be strong enough to override selection from predation or competition (e.g. Edeline et al. 2007; Kuparinen and Merilä 2007; Eikeset et al. 2016).

Our results suggest that if predation is strong in early life stages and delayed maturation can help to outgrow this window, evolutionary effects of fishing can be particularly strong, as in some middle sized species (species 4 and 6). However, due to this predation versus fishing "tug of war" evolutionary impacts of fishing are not manifested until fishing mortality becomes relatively high (in species 4). Nevertheless, in one middle sized species (species 5) fishing did not reduce maturation size, as selection from predation, and possibly slightly improved food availability at slightly larger sizes (Fig.S.2) outweight the selection from fishing. While this may look like good news, such species might be particularly vulnerable to long-term exploitation, unable to improve their fitness by evolving towards earlier maturation.

For large bodied species the effect of fishing followed our expectations. In agreement with observations that harvesting imposes very strong selective pressures (e.g. Wood et al. 2018), fishing completely reversed natural selection gradients (in more realistic simulations with predation enabled) and led to a rapid evolutionary response of maturation size. The actual rate of response in our simulations cannot really be compared to real world ecosystems, because generation time, levels of phenotypic diversity and the genetic inheritance mechanisms in the model, do not accurately represent those in real fish populations. Nevertheless, the fastest rates of change observed in our model are broadly compatible with rates of change in empirically observed fish stocks or those predicted in ecogenetic models with more accurate evolutionary mechanism. The fastest rates observed in our simulations occur after the introduction of fishing, and are in the range of 50% in 300 years or 0.17% per year (Fig.2.2b-d). In intensively fished stocks (F values similar to our baseline simulations) observed rates of phenotypic change are 1% per year, but this rate is likely to include both evolutionary and plastic trends. The rate

(1% per year) is about four times faster that evolutionary rates reported in various population and ecogenetic models (Audzijonyte et al., 2013b), which is also compatible with our findings. The important result is that the evolutionary response occurred even at the instantaneous fishing mortality of $0.1yr^{-1}$, which is generally considered a low level of fishing mortality, below levels that are consistent with maximum sustainable yield (Blanchard et al. 2014, www.ices.dk). This finding is consistent with other evolutionary models demonstrating that even low levels of fishing will select for smaller maturation size (e.g. Andersen et al. 2007).

Model limitations and future work

Although this study and modelling exercise is seemingly complex, it is a substantial simplification of real marine ecosystems. The fishing scenarios explored target all species with similar size selectivity and intensity and were stable through time. The initial set of species was spaced evenly over size categories and had shared diet preferences and other physiological parameters. None of this is true in the real world. We used an initial maturation size value of a quarter of the asymptotic size (Andersen and Pedersen, 2010; Hartvig et al., 2011) but different and even multiple optima may exist for species of different sizes. The evolutionary mechanism itself is highly simplified and does not include trait recombination or covariances, and each phenotype only produces offspring identical to itself. This means that selection differentials from the model cannot be compared to empirical studies. Finally, even though we included survival cost of reproduction, the full set of reproductive costs may still be too small. This could explain very small evolved maturation sizes in species – if a threshold amount of energy is required to achieve maturation, it would set a limit on how small maturation size could be. Indeed, a model with energetic cost of reproduction included (Audzijonyte and Richards, 2018) predicted a more realistic and larger maturation size of intensively fished Baltic Sea cod than a model without such costs (Andersen et al., 2007). Yet, despite these simplifying assumptions, we found a general emergent pattern of a conserved ratio of maturation sizes and maximum sizes that was consistent with empirical values (Fig.2.6). Our observed evolutionary rates were also broadly compatible with those expected in wild stocks. The range of η values from our model fell within the empirical range, noting that those values were obtained from species' maturation weight

and weight at infinity from empirical von Bertalanffy relationships. Future studies would be worthwhile to further assess whether the predicted changes and timescales involved would still hold under more realistic species composition, traits, diets, and more realistic fishing scenarios.

Conclusion

One of the key questions in our study was to assess whether predation-driven selection could counteract or even reverse fishing induced evolution (FIE). In this size and trait-based food-web model, the answer is that this is generally not the case, although it depends on the size of the species considered and fishing intensity imposed. Our findings suggest that for the largest species, harvesting, even at low intensity, imposes very strong selection because they have low predation mortality at around and above their maturation size. In contrast, the smallest species may be mostly limited by food availability, and neither predation nor fishing affect their fitness landscapes substantially. Such species may be already maturing close to their physiological or ecological limit, especially if cost of reproduction is considered (e.g.Audzijonyte and Richards 2018). This shows the importance of simultaneously considering bottom up processes (e.g. food availability) when looking at FIE, and highlights the benefits of physiologically structured multi-species models where growth and reproduction are dependent on food availability. Finally, the most unpredictable eco-evolutionary responses emerge in medium sized species, sandwiched between larger predators and smaller competitors. For these species, selection pressures from fishing, predation and competition fluctuate through time and here predation release may indeed occasionally balance the selection from fishing. These findings call for more empirical studies on the possible evolutionary trends in medium sized species, improved understanding of interactive forces of selection, and stronger precautionary measures to minimise FIE in large fish.

Authors' Contributions

RF, JLB and AA conceived the ideas, designed methodology, and led the writing of the manuscript; RF collected and analysed the data. All authors contributed critically to the development of the study, drafts and gave final approval for publication.

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Data accessibility

The model open source code and data are available on https://github.com/baldrech/MizerEvo.

2.6 Tables

TABLE 2.2: Model equations for each species' ecological dynamics. Subscripts for each species are not included in the equations below for readability. These dynamics also hold for each phenotype (nested within each species) once they have entered the size spectrum. Equation numbers reference the processes illustrated in Figure 2.1 and descriptions in main text. $N(m)$ is the density at size driven by: $g(m)$ which is the feeding dependent growth rate at size and $\mu(m)$ which is the mortality at size, the latter is comprised of several mortality terms below. All parameter values and definitions are provided in Table 2.3 or the main text.

Equation	Description	
Species population dynamics	$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$	(E1)
Background resource dynamics	$\frac{\partial N_R(m,t)}{\partial t} = r_0 m^{p-1}\left[\kappa_R m^{-\lambda} - N_R(m,t)\right] - \mu_p(m)N_R(m,t)$	(E2)
Prey size selection by size m predator	$\phi(m, m_p) = exp\left[\frac{-(ln(m/(\beta m_p)))^2}{2\sigma^2}\right]$	(E3)
Encountered food by size m predator across all sizes (mp) of species j prey	$E(m) = \gamma m^q \int \left(N_R(m_p) + \sum_j \theta_j N(m_p)\right)\phi(m, m_p) m_p \mathrm{d}m_p$	(E4)
Feeding level	$f(m) = \frac{E(m)}{E(m) + hm^n}$	(E5)
Somatic growth	$g(m) = (\alpha f(m) h m^n - k_s m^p)(1 - \psi(m))$	(E6)
Energy allocation towards reproduction	$\psi(m) = \left[1 + \left(\frac{m}{m^*}\right)^{-u}\right]^{-1}\left(\frac{m}{M}\right)^{1-n}$	(E7)
Reproduction	$R_p = \frac{\epsilon}{2m_0}\int N(m)(\alpha f(m) h m^n - k_s m^p)\psi(m)\mathrm{d}m$	(E8)

Recruitment	$$R = R_{max}\frac{R_p}{R_p + R_{max}}$$	(E9)
Predation mortality on size mp prey inflicted by all sizes (m) of species j predators	$$\mu_p(m_p) = \sum_j \int \phi(m, m_p)(1 - f_j(m))\gamma_j m^q \theta_j N_j(m)\mathrm{d}m$$	(E10)
Senescence mortality	$$\mu_{se} = \begin{cases} se_{min} + (se_{max} - se_{min})e^{-\frac{M}{m}}, & \text{if } m > m^* \\ 0, & \text{otherwise} \end{cases}$$	(E11)
Starvation mortality	$$\mu_{st} = \begin{cases} st_r m\left(k_s m^p - \alpha f(m) h m^n\right), & \text{if } k_s m^p > \alpha f(m) h m^n \\ 0, & \text{otherwise} \end{cases}$$	(E12)
Background mortality	$$\mu_b = \mu_0 M^{n-1}$$	(E13)
Fishing mortality	$$\mu_f = \begin{cases} 0.8, & \text{if } m >= m^* \\ 0, & \text{otherwise} \end{cases}$$	(E14)

TABLE 2.3: Parameters table. M is noted "variable" as it is species specific (values in Table 2.1). η starts at 0.25 for all species but will evolve during the simulations. Parameters values are taken from Hartvig et al. (2011). The value from γ was calculated from: $\gamma = h\frac{f_0}{\sqrt{(2\pi)}\sigma\beta^{\lambda-2}e^{((\lambda-2)^2\sigma^2/2)}\kappa(1-f_0)}$ (Hartvig et al., 2011). Initial values for the abundance density $N(m)$ of each species at $t = 0$ were based on the equilibrium equation: $N = \frac{\kappa}{1000}M^{(2n-q-2+0.35)}m^{(-n-0.35)}$ provided in Andersen and Beyer (2006).

Symbol	Value	Units	Parameter
Individual growth			
M	variable	g	Asymptotic size
η	0.25	-	ratio between M and m^*
m^*	ηM	g	Maturation size
f_0	0.5	-	Initial feeding level
γ	538	$g^{-q}m^3yr^{-1}$	Factor for search volume
α	0.6	-	Assimilation efficiency
h	85	$g^{1-n}year^{-1}$	Maximum food intake
n	0.75	-	Exponent for max. food intake
p	0.75	-	Exponent for standard metabolism
ks	4	-	Factor for standard metabolism
β	100	-	Preferred predator-prey mass ratio
σ	1	-	Width of the feeding kernel
q	0.8	-	Exponent of search volume
Reproduction			
m_0	0.1	mg	Offspring mass
ϵ	1	-	Efficiency of offspring production
u	7	-	Width of maturation transition
Mortality			
ξ	0.1	-	Fraction of energy reserves
μ_0	2	$g^{1-n}year^{-1}$	Background mortality
se_{max}	1	$g^{1-n}year^{-1}$	Upper limit for senescence mortality
se_{min}	0.1	$g^{1-n}year^{-1}$	Lower limit for senescence mortality
st_r	0.1	$year^{-1}$	Starvation mortality cost
θ	variable	-	Interaction matrix species-specific value
Resource spectrum			
κ	0.05	$g^{\lambda-1}m^{-3}$	Magnitude of resource spectrum
λ	$2-n+q$	-	Slope of resource spectrum
r_0	4	$g^{1-p}year^{-1}$	Regeneration rate of resources
m_{cut}	1	g	Upper limit of resources spectrum
Evolution			
χ	0.001	-	Phenotype's introduction probability
Ω	10^{-30}	$individual/m^3$	Extinction threshold
	5%	-	Fraction of initial phenotype's abundance
	$+-20\%$	-	Magnitude of trait evolution

Chapter 3

Emergence of large predator-prey mass ratio in a size-structured eco-evolutionary model

3.1 Summary

Predator-prey interactions define food web structure. In marine ecosystems, these interactions are based on size, which can be evaluated using predator-prey mass ratios (PPMR). Constraints on PPMRs, due to energy needs and gape size, suggest that intermediate PPMRs of $\sim 10^2$ will characterise marine food webs. However, observed PPMRs range from 1 to 10^7 in marine ecosystems, with most PPMRs being under 10^3. Resource availability has the potential to influence PPMRs, via changes in food chain length and ecosystem trophic structure. However, the effect of resource availability on the emergence of different PPMRs, are poorly understood, including the conditions under which large predators with large PPMRs ($> 10^3$) are favoured in ecosystems. Here, we used a size-structured model incorporating eco-evolutionary dynamics, to explore sized-based interactions, and tracked the emergence of different PPMR values in a multi-species ecosystem across varying levels of resource availability.

We used three scenarios of increasing resource availability yielding communities adapted to low, medium and high resource availability. We found that reducing resource availability

triggers a shift to larger PPMRs across all species in the simulations, with larger species reaching the largest PPMR values. Only high resource availability led to PPMR <= 10^2 for the largest species (piscivorous predator), however the community metrics (i.e. size spectrum slope and trophic transfer efficiency) stayed relatively similar across scenarios. The model yielded realistic PPMR adaptations, meaning that modelling eco-evolutionary feedbacks within the size-structured framework can help understand how predation interactions and resource availability determines food-webs trophic structure.

Keywords

eco-evolutionary model, evolution, multi-species size spectrum model, predator-prey mass ratio, diet, marine food webs

3.2 Introduction

Ecosystem functioning depends on the structure of food webs (Thomas et al., 2012) and food webs depend on predator-prey interactions (Allesina and Tang, 2012). Predator–prey interactions typically depend on body size, especially in aquatic ecosystems, and an important concept that links predator–prey interactions to size-dependent interactions is the 'predator–prey mass ratio' (PPMR) (Brose, 2010; Nakazawa et al., 2011; Kalinkat et al., 2013). PPMRs are constrained by energy requirements - predators cannot feed on prey that is too small due to insufficient energy gains, and gape size - predators are unable to capture and subdue prey that is too big (Wainwright and Richard, 1995). These limitations lead to an expectation that most PPMRs will exhibit intermediate values in the range of 100 to 1000 (Brose, 2010), and this assumption has been widely used in size-based theory predictions and food-based models. For example, assuming a typical PPMR of 100 – 1000 has led to predictions that large marine species will be at a trophic level of 5 or 6 (Andersen, 2019) and that expected average fish biomass in the world ocean's is ca $2.8 g/m^2$ (Jennings and Warr, 2003).

In contrast with theoretical support for an intermediate range of PPMRs in ecosystems, a recent study showed that observed PPMRs in aquatic ecosystems range from 1 to 10^7 (Brose et al., 2019). For example, reefs and open-water pelagic ecosystems can be dominated by species with very large PPMR values such as larvaceans, tunas, baleen whales, whale sharks and some reef fish (Barnes et al., 2010; Wirtz, 2012; Tucker and Rogers, 2014; Heneghan et al., 2016; Kiørboe, 2016). The drivers of these large observed PPMRs remain poorly understood. Brose et al. (2019) suggested that on a global scale PPMR values can be largely predicted from predator traits and ecosystem type, such as lakes, streams, land and marine. These factors provide important explanatory power, but there remains a lot of unexplained variation in marine ecosystems.

Addressing this lack of understanding around the drivers of PPMR is critical as these ratios affect energy transfer efficiency (Barnes et al., 2010), food chain length (Jennings and Warr, 2003) and food web stability (Law et al., 2009). For example, size-based models have shown that high community-level PPMRs decrease the stability of communities (Blanchard et al., 2008; Law et al., 2009): oscillations in the smallest size classes are immediately reflected in the biomasses of large organisms feeding on these small size classes. Also, trophic transfer efficiency between trophic levels decreases with increasing PPMR (Barnes et al., 2010) and shortens the food chain length across the community (Jennings and Warr, 2003). This has implications for the abundance of fish that a given level of resource productivity can sustain, and will determine fisheries productivity. Thus, understanding the factors that determine PPMRs is central to understanding the structure and dynamics of food webs (Yvon-Durocher et al., 2011; Gravel et al., 2013; Trebilco et al., 2013; Chang et al., 2014). It is critically important to understand why very large and small PPMRs evolve in different systems and species and the effect of these variations on community structure and function. To address this, in this study, we use a size-based model to explore the evolution of different PPMRs and the consequences for community structure and function.

We hypothesise that resource availability will impact PPMRs and drive a greater range of ratios that energy and gape size constraints imply. PPMR affects the number of trophic levels and trophic transfer efficiency, thus resource availability is likely to determine the food chain length

and optimal PPMR values. Larger PPMRs allow predators to access more abundant, relatively smaller prey, but this usually comes at the cost of search and handling time and nutritional value (Vucic-Pestic et al., 2010). To explore this hypothesis, we used a dynamically evolving size-structured multi-species model to explore evolution of PPMR strategies in swimming vertebrate predators across a range of resource abundance levels. The key aspect of this study is the dynamic and selection driven evolution of the PPMR in multiple species in an ecosystem, where species interactions are strongly dependent on size. PPMR is represented as an individual-level evolving trait, and we explored how this evolution is determined by the resource availability, different levels of trade-offs with feeding efficiency, and species interactions. We found that our model reproduces empirically observed PPMR values across species of different body sizes, and that resource availability was a key driver of large PPMRs, particularly in the largest species.

3.3 Methods

At the core of this study are the eco-evolutionary processes integrated into a physiologically structured trait-based size-spectrum model. The size-spectrum modelling framework we used is based on Andersen and Pedersen (2010); Hartvig et al. (2011) and is available as the R package "mizer" (Scott et al. 2014; https://sizespectrum.org/mizer/), while the eco-evolutionary dynamic is available as an additional integrated "mizer" component (Forestier et al. 2020, mizerEvolution). Below we briefly describe these components, but further details on our coupled model and its assumptions are available on the mizer website (https://sizespectrum.org/mizer/) and in chapter 2. All code to replicate our analysis is available at mizerEvoMerging.

3.3.1 Ecological component

Size spectrum models are physiologically structured models that track the density of individuals at size through time (Andersen, 2019). Growth, maturation and reproduction are all food-dependent, and driven by size-based feeding interactions. The preference of a predator for a prey size is expressed in terms of the ratio between the weight of the predator and the weight of its prey, a relationship called Predator Prey Mass Ratio (PPMR) and, in our model, described

by the parameter β. The feeding kernel determines feeding relationships in the model and is informed by β, which defines the centre of the feeding kernel, and an additional parameter σ, which describes the width of the feeding kernel. Feeding, growth, mortality and reproduction occur at every time step. The model therefore assumes continuous reproduction. The population dynamics of the species is then obtained by solving the conservation equation (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$$

where m is the species mass, $g(m)$ is the individual growth, and $\mu(m)$ is the mortality (Table 3.1, E2).

Growth depends on the available food coming from prey within the explicitly modelled size-structured (fish) components and a background resource, which is modelled using a semi-chemostat growth assumption and assumed here to extend between the size of 10^{-10} to $1g$ (bacteria to zooplankton) (Table 3.2). Consequently, all individuals are simultaneously predator and prey. Mortality is a combination of predation mortality, senescence mortality (Table 3.1, E11), starvation mortality (Table 3.1, E12) and a constant background mortality (e.g. diseases - Table 3.1, E13). Predation is the main source of mortality, while senescence, starvation and background mortality limit population growth and thus allow species to coexist. Smaller individuals are assumed to have higher background mortality rates.

3.3.2 Eco-evolutionary dynamics

Modelled species differed by their asymptotic size only, and each species was represented as a pool of phenotypes (exact copies of each other apart from the evolving trait, PPMR). Throughout the simulations, each species' PPMR was allowed to evolve. This meant that at each time-step, there was a probability χ (Table 3.2) that an existing phenotype ("parent") generates a new phenotype characterized by a different PPMR with a value randomly sampled from a normal distribution centered on the parent's PPMR and with a standard deviation of ζ (Table 3.2). This

method gave an average maximum change in PPMR per species of 1.5% per year. The species' PPMR was calculated as the mean of its phenotypes, weighted by the phenotypes' abundances.

The number of phenotypes per species is an emergent property of the model. Phenotypes behave like independent species in that they compete for food, grow, reproduce and die; hence their number per species depends on food availability and bioenergetic processes. Recruitment, in particular, effect phenotypes abundance. In our model, recruitment is density dependent, the relationship describing this process is parameterized to allow coexistence of multiple species, and it is first estimated at the species level. All phenotypes are pooled together to calculate their species' spawning output and density-dependent recruitment parameter. Then, the species' recruits are allocated to each phenotype proportionally to the phenotype's abundance. For more details on the evolutionary component see chapter 2 and Forestier et al. (2020).

3.3.3 Assumptions about PPMR evolution

In trait-based size-spectrum models, predation is size-dependent. The preference of a predator for a prey size is expressed using PPMRs relationship. The feeding kernel which determines feeding relationship in the model is composed of β, which defines the centre of the feeding kernel, and an additional parameter σ which describes the width of the feeding kernel.

The β parameter explored here refers to the preferred PPMR" as opposed to the "realised PPMR" (Tsai et al., 2016). The realized PPMR is typically estimated through analyses of stomach content data and it is used to estimate preferred PPMR as approximately 60% of the mean realized PPMR (Hartvig et al., 2011), i.e. realised prey sizes are smaller than the preferred prey sizes as high PPMR values mean smaller preys. Preferred PPMR is used as input parameter to model feeding kernels. In this study we consider realized PPMR only when comparing model output with empirical data (see section – community metrics).

In this study we assumed that all species parameters, except β (and α due to their trade-off; see below), remained fixed. This was to reduce the number of interacting parameters characterizing each trait that affect evolutionary trajectories and thus to isolate the ramifications of changing PPMR on the fish traits and the whole community. However, this meant that changes in key

parameters linked to β and influencing predatory interactions, such as σ (width of the feeding kernel), or food availability, such as γ (volumetric search rate; Table 3.2) remained fixed. We also assume that β remains constant throughout an individual's life, hence we overlooked ontogenetic shifts in PPMR. These assumptions meant that species could exhibit a shift in their PPMR through time, but that the shape of their feeding kernel remains constant. While there could be reason to suspect co-variation between σ and β (Law et al., 2009), we did not find empirical support for this (Barnes et al., 2010) and, for simplicity, we held the shape of the feeding kernel constant across species and simulations.

Evolution of any trait is limited by trade-offs. Recognising these trade-offs is a critical part of evolutionary models (Litchman et al., 2007). In this study we assumed that higher PPMR values trade-off with lower assimilation efficiency (α)(Welch, 1968). Such trade-off aims to constrain the adaption of the studied trait to prevent it from reaching unrealistic values (e.g. constant adaptation towards higher PPMR values) and aimed to account for the increasing activity cost required to forage and handle very small prey, and the predominantly smaller volume to surface ratio of small prey, leading to lower nutritional content (e.g. Barnes et al. 2019). The advantage of large β values is that predators can feed on small organisms, which are more abundant and in our model also include the background spectrum. We assumed that assimilation efficiency (α) decreases with increasing (β) as

$$\alpha = 0.6x/(y + log_{10}\beta)$$

We performed 2 sets of simulations to assess the sensitivity of the β/α trade off. The trade off used in the first set of simulations, which is the focus of this study, was set as $x = 3$ and $y =$, resulting efficiency ranged from 0.9 at $\beta = 10$ to 0.3 at $\beta = 10^5$. The second set consisted of a sensitivity analyses where we explored alternative trade-off values. Specifically, we considered either similarly high α at low β and steeper decrease in α with increasing β, or lower α at low β values, and less steep decrease (Fig.3.4 and Table S.1).

3.3.4 Simulation design and effect of resource availability

Our model included 5 species with asymptotic size uniformly spread on a logarithmic scale between 10 to $10^4 g$. We set the species' PPMR to 1000 and we calculated their initial abundance based on the equilibrium conditions (Andersen and Beyer, 2006), which uses feeding and carrying capacity parameters (Table 3.2). Then, we ran the model 100 years forward without the eco-evolutionary dynamic to reach a stable state and we randomly spread each species' biomass at stable state across 20 phenotypes (following the rules described in the above section). Last, we ran the updated model 1000 years forward with eco-evolutionary dynamic to let the species biomass reach a new stable state. The 1000 years was deemed as sufficient simulation time, as trait values settled around an equilibrium long before the end of the simulations.

We explored the PPMR evolutionary trends among different size-structured species under different resource availability settings. To do so, we ran three sets of 50 simulations with different values of κ (resource availability, Table 3.2). This parameter determines the carrying capacity of the background spectrum and therefore resource availability for the fish community. The 50 simulations per each κ value were needed to account for the stochastic nature of evolutionary process.

3.3.5 Assessing community metrics

We used community metrics to compare the simulations outputs. Specifically, we calculated the slope of the community size spectrum, the mean realised PPMR (β_r), and the trophic transfer efficiency (T_e). We used a linear regression method to calculate the slope of the community size-spectrum, and we considered all species and phenotypes but excluded individuals smaller than $10g$. We used the emergent predator diets to estimate the β_r for each species as the size ratio between the most commonly eaten prey sizes per predator size. We then averaged these values across species and size classes. We calculated trophic efficiency at the community level following Barnes et al. (2010):

$$T_e = \beta_r^{(\lambda+1+n)}$$

where λ the slope of the spectrum and n the exponent for maximum food intake, here assumed to be 0.75 (3.2). The trophic transfer efficiency is the ratio between the production received by a trophic level from the trophic level below and the production it delivers to the trophic level above. We estimated the realised PPMR of each species based on the model's output diets which allowed us to compare it to the empirical PPMR data from Barnes et al. (2010) in terms of PPMR versus asymptotic size trends.

3.4 Results

In this study, we explored the emerging PPMR under different resource availability values (κ) (i.e. low κ decreases the carrying capacity of the background spectrum and therefore the overall resource availability). PPMR started at 1000 for every species and each κ. Traits and biomass variations quickly reached equilibrium (except species 1 when $\kappa = 0.2$) (Fig.3.1-3.2).

3.4.1 Evolution of PPMR across species body size and resource levels

Across all levels of resource availability and simulations mean preferred PPMR increased with asymptotic size (i.e. larger species adopt higher PPMR) except in the case of the largest species where two PPMR strategies emerged (species 5, Fig.3.3). One PPMR strategy, captured a "large planktivore" strategy with high values of PPMR at large asymptotic size, particularly evident at low resource levels (Fig.3.3). The largest species' PPMR was one order of magnitude greater than that of the smallest species (5000 vs 400) when resource availability was low ($\kappa = 0.05$; Fig.3.3a,m) and two orders of magnitude greater when resource level was higher (3000 vs 70 with $\kappa = 0.1$ and 1000 vs 10 with $\kappa = 0.2$; Fig.3.3b,n & c,o). The other PPMR strategy we described as a "piscivory" strategy with much lower PPMR values at large asymptotic size, yielded the lowest PPMR in the ecosystem for all levels of resource availability (κ). The PPMR gap between these two strategies was wide at low levels of resource availability, but progressively closed with increasing κ. Broadly, the slopes of the relationship between median species PPMR versus asymptotic body size increased with resource levels. However, as resource availability

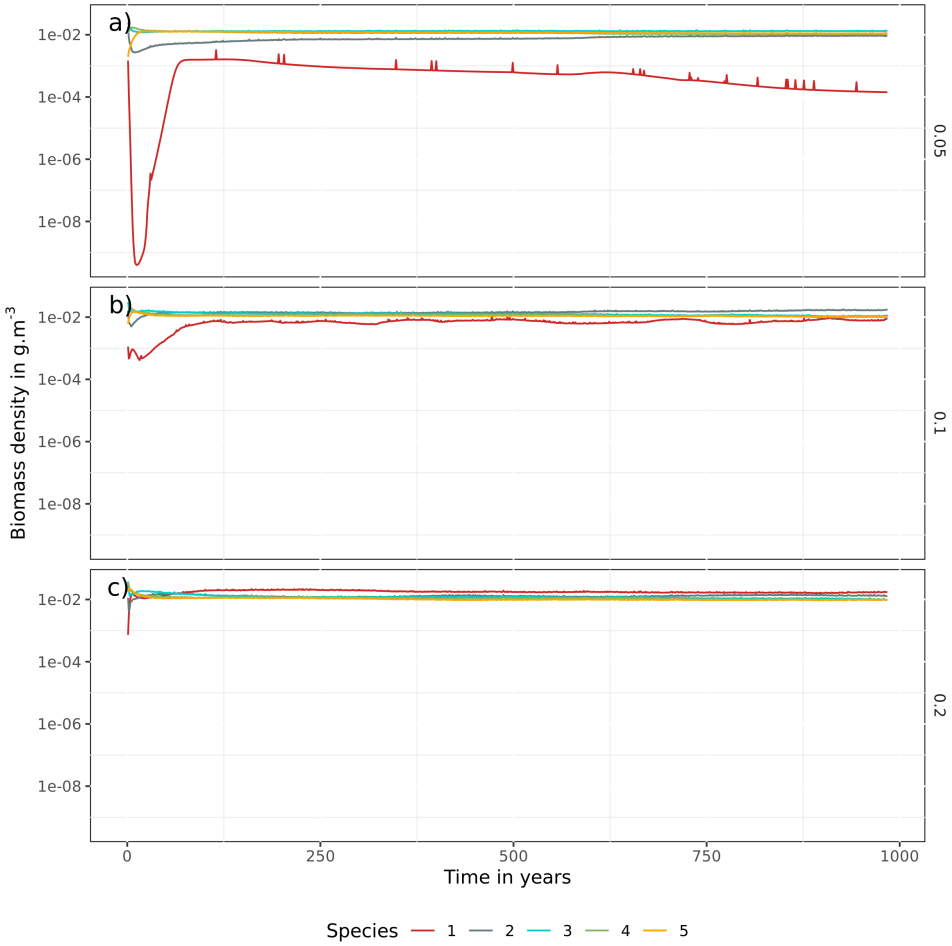


FIGURE 3.1: Biomass variation through time across resource scenarios. The solid line is the mean value per species across simulations. κ is indicated on the right-hand side of the plot. Species are ordered from smallest to largest.

increased (higher κ), PPMR decreased across all species (intercepts decreased with increasing κ).

The biomass of low PPMR phenotypes for species 5 varied across values of κ: low resource availability led to decreases in PPMR, and also decreased the proportion of "piscivore" phenotypes in species 5 (Fig.3.3m). Thus, at low κ there were few "piscivore" phenotypes, and for those "piscivore" phenotypes, the PPMR was low, close to 10. In contrast, at high κ there were more "piscivore" phenotypes but those "piscivore" phenotypes had a higher PPMR (Fig.3.3o).

The “piscivory” strategy in species 5 only emerged when the assimilation trade-off yielded high α values on average (Fig3.4). Trade-offs c) and e) had on average lower α output compared to trade-off a) (the default trade-off used in the main set of simulations) where no “piscivory”

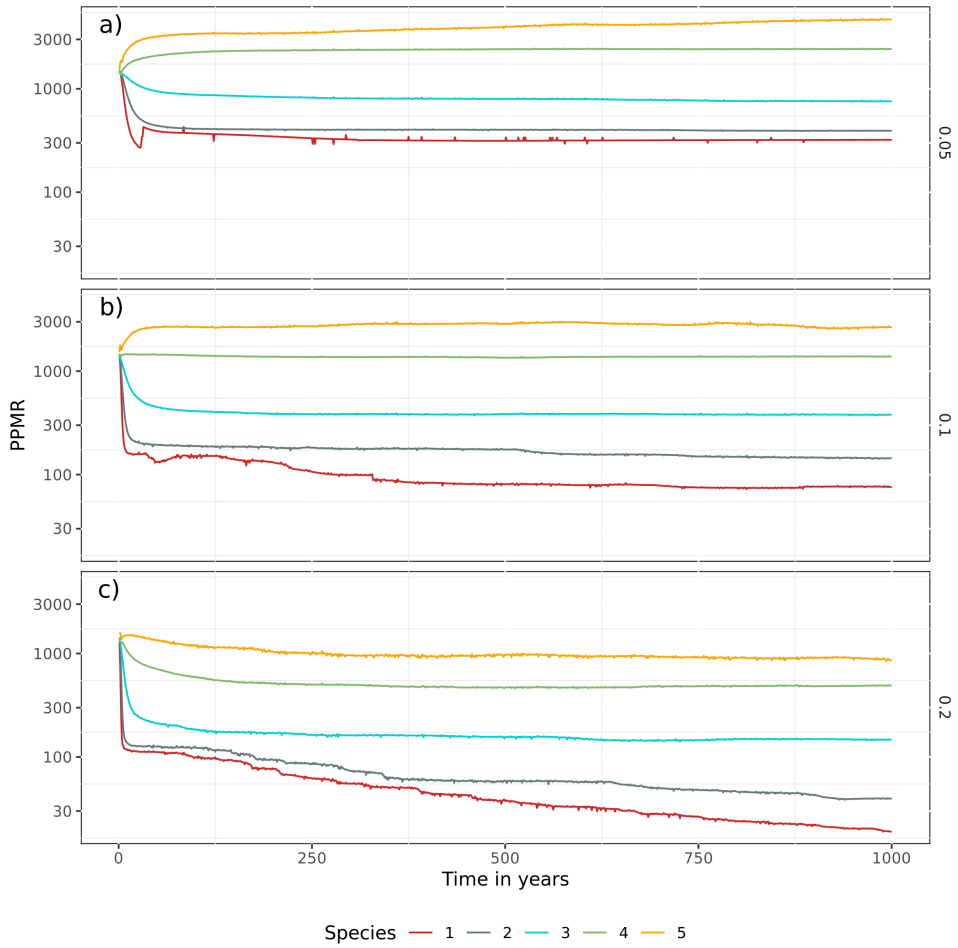


FIGURE 3.2: PPMR variation through time across resource scenarios. The solid line is the mean value per species across simulations. κ is indicated on the right-hand side of the plot. Species are ordered from smallest to largest.

strategy emerged whereas both trade-offs b) and d) had on average higher α output and allowed "piscivory" to emerge in species 5.

The resource availability only affected the number of phenotypes coexisting within the three largest species (Fig.3.5). Species 3 and 4 had more phenotypic diversity at low resource level ($\sim$ 30 phenotypes Fig.3.5a) whereas species 5 had the most at the high resource level ($\sim$ 40 phenotypes Fig.3.5c). At intermediate resource level, these three species had approximately the same amount of phenotypes each ($\sim$ 20 phenotypes Fig.3.5b) .

The pattern of increasing PPMR with asymptotic size was consistent with the broad-scale empirical data from Barnes et al. (2010), when the realised modelled PPMR values were calculated by species for each simulation and pooled across resource levels (Fig.3.6). However,

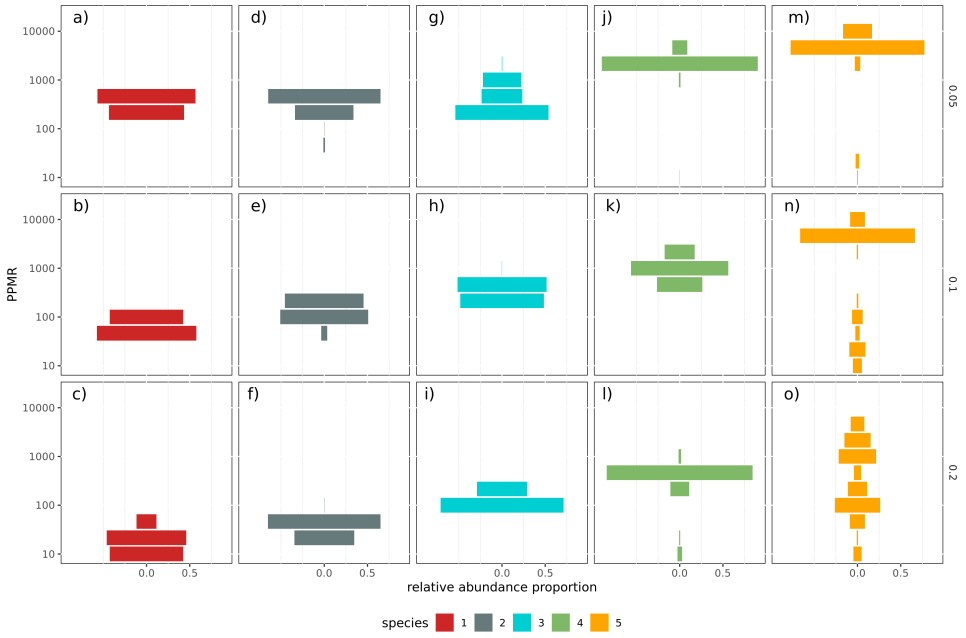


FIGURE 3.3: Bar plot of the PPMR values at the end of the simulations per species and κ (resource availability increases with κ value). Species are ordered by asymptotic size (species 1 is smallest while 5 is largest). Bars are mirrored along the y-axis. κ is indicated on the right-hand side of the plot.

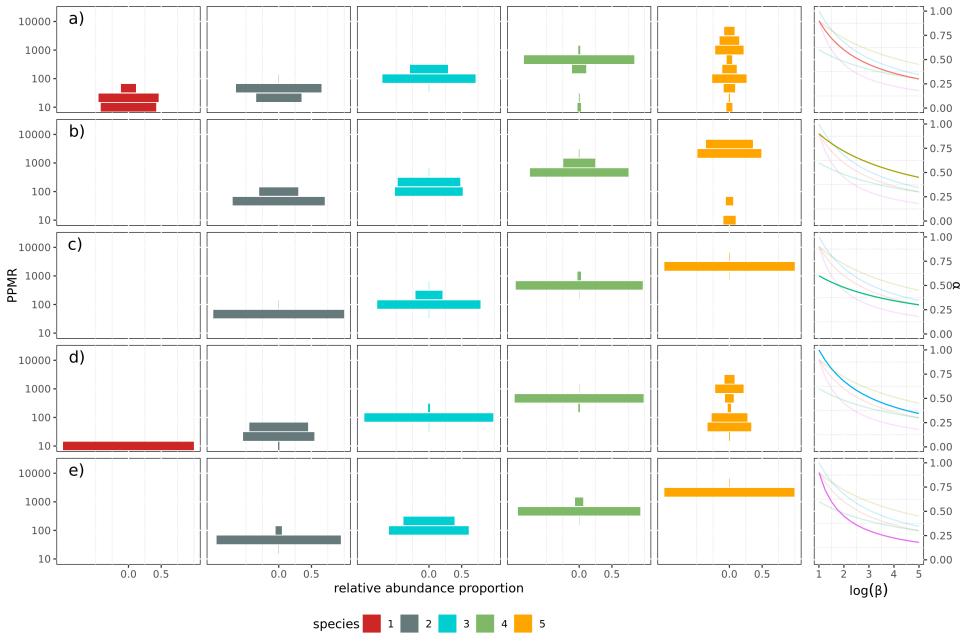


FIGURE 3.4: Bar plot of the PPMR values at the end of the simulations per species at $\kappa = 0.2$ (highest resource availability). Species are ordered by asymptotic size. Bars are mirrored along the x-axis. The left column shows the corresponding assimilation trade-off used to run the simulations.

the pattern of increasing median PPMRs was more marked in the modelled predictions than the observations (Kruskal-Wallis significance test: $x2 = 7077.5$; $p_{value} < 2.2.10^{-16}$). The variation

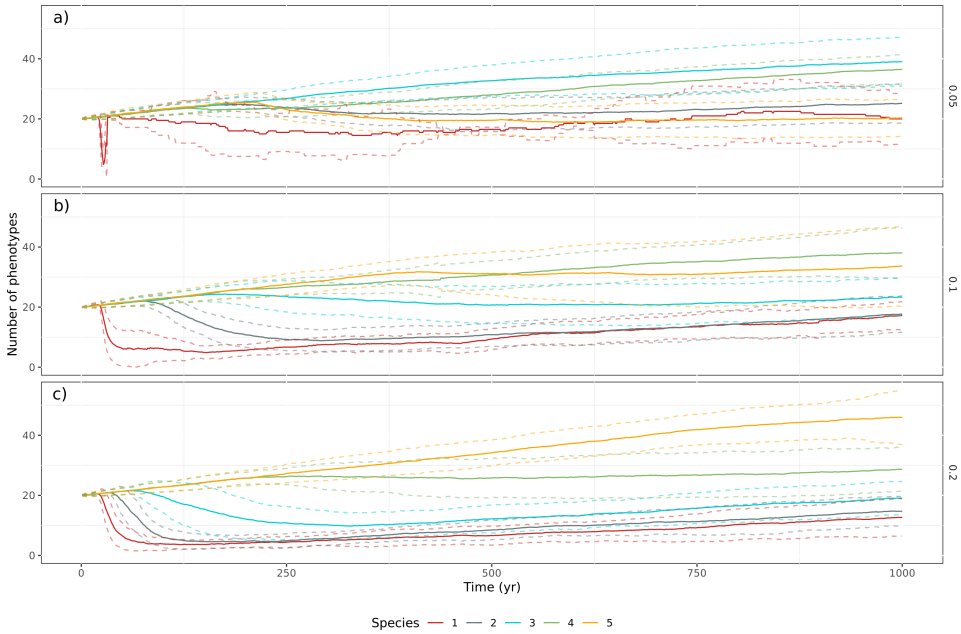


FIGURE 3.5: Number of phenotypes through time across resource availability scenarios. The solid line is the mean value per species across simulations and dashed line is the standard deviation of the mean. κ is indicated on the right-hand side of the plot. Species are ordered from smallest to largest.

in the empirical data was wider than the model, especially at lower PPMR values perhaps owing to many different individuals, species, and ecosystem sampled.

3.4.2 Energy transfer in communities

Three indicators were used to classify and compare the different communities across scenarios: the slope of the size spectrum λ, the mean realised PPMR β_r and the trophic transfer efficiency (Fig.3.7). Varying κ and thus the species PPMR (as observed in Fig.3.3) – affected λ with lower λ resulting in a shallower spectrum (Fig.3.7a). β_r decreased with increasing κ (Fig.3.7b). We calculated the trophic transfer efficiency using λ and β_r (Fig.3.7c). The resulting transfer efficiency was well within what is observed in the wild, as empirical data range from 0.3% to 52% ranging from poles to tropics (Rosenberg et al., 2014). High λ and low β_r gave the most efficient trophic transfer, but transfer efficiency was most sensitive to small variations in λ (estimated from the community size spectrum using linear regression with a mean R^2 of 0.96). Thus, median transfer efficiency was greatest at the lowest resource availability (resulted in the highest λ) and then the highest resource availability (resulted in lowest β_r and moderately high

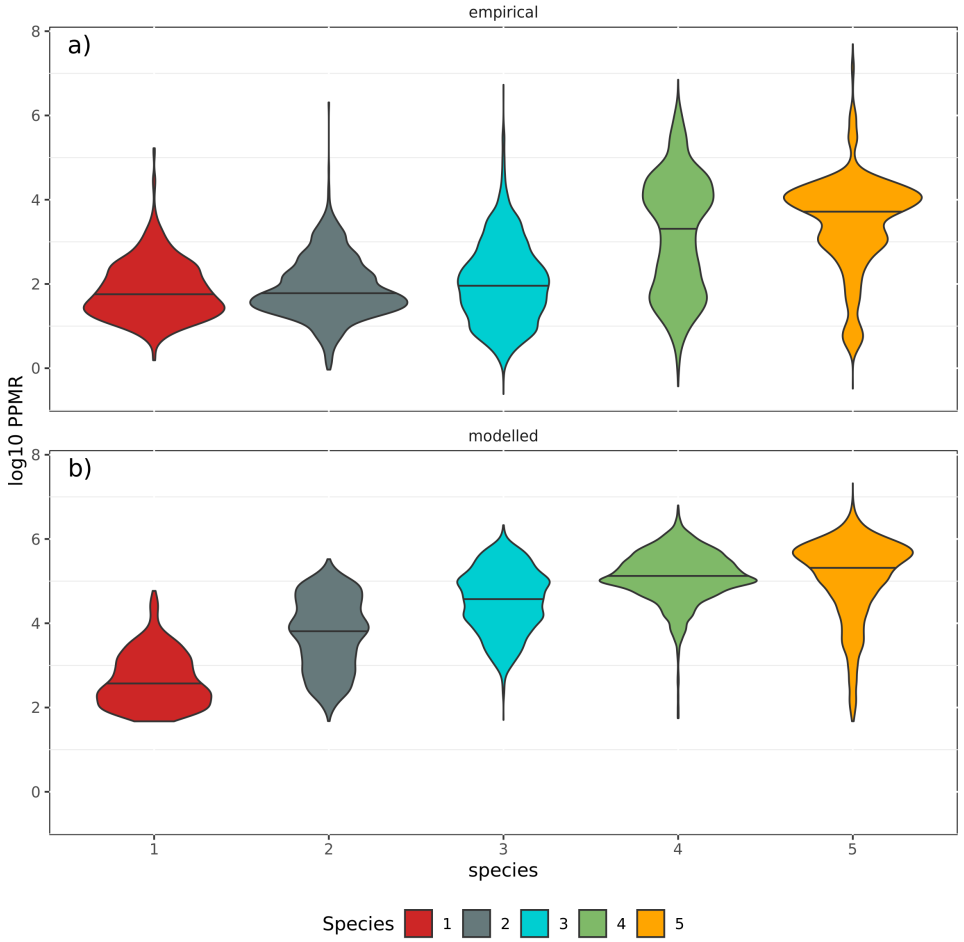


FIGURE 3.6: Comparison of empirical data of PPMR from Barnes et al. (2010) (panel a) versus modelled results (panel b). For easier comparison, the empirical data in a) is grouped in functional groups of similar asymptotic size as the species modelled in b). The modelled results are adjusted to show realised PPMR to be able to compare to the empirical data using the assumption that preferred PPMR is 60% of realised PPMR (Hartvig et al., 2011). The horizontal lines within the violins show the median value.

λ).

3.4.3 Diet composition of large predators

To understand differences between the two feeding strategies of species 5, we explored variation in diet composition among phenotypes (Fig.3.8). High PPMR values represented almost exclusively "planktivore" forms (here as defined by solely feeding on the resource spectrum) of species 5, with "piscivorous" diets only occurring at the largest size (close to $10^4 g$) when there was the highest resource availability (i.e. high λ) (Fig.3.8c). In the model, predation is

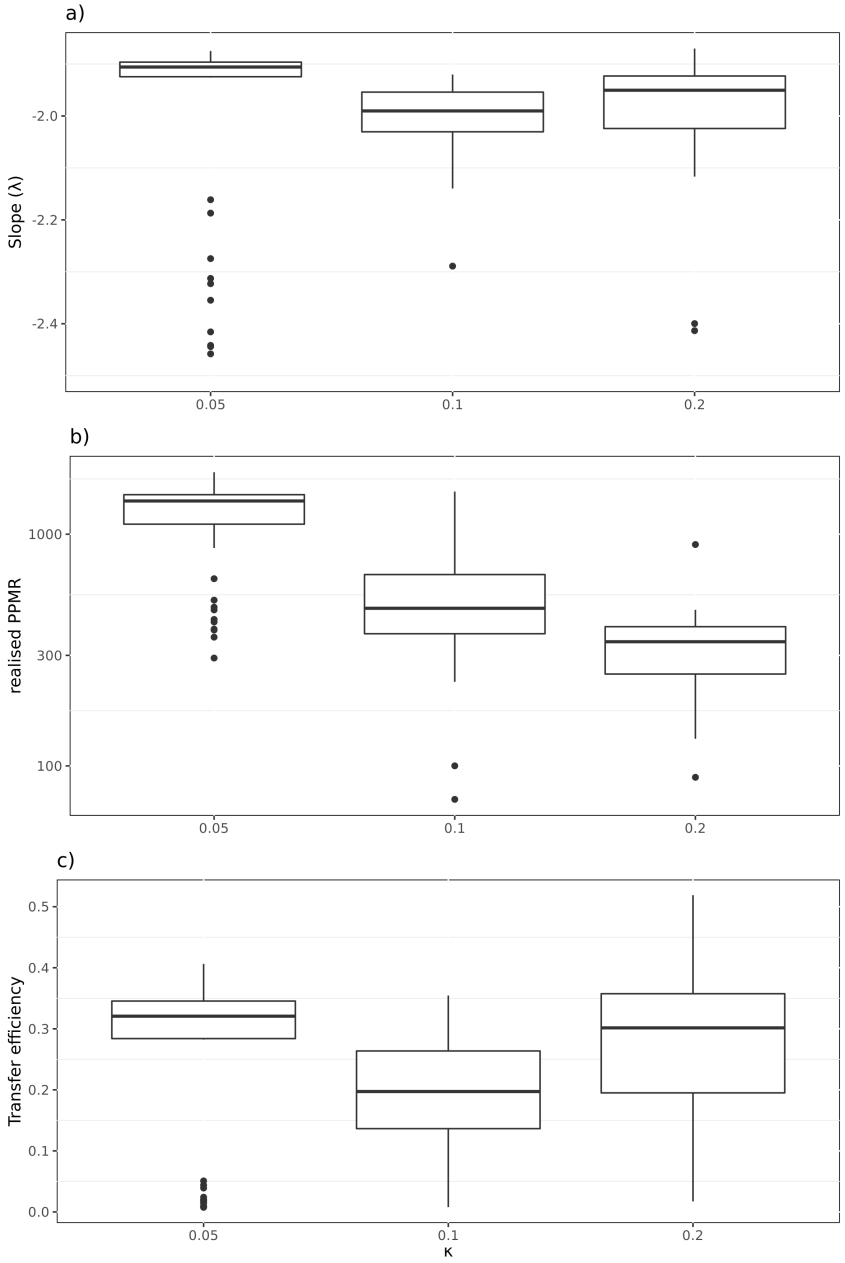


FIGURE 3.7: Boxplot of three indicators of food web structure at different levels of resource availability (κ), averaged across simulations. a) the steepness of the community size spectrum λ. b) the community PPMR β_r. c) the trophic transfer efficiency. Black dots are outliers and horizontal lines are medians.

proportional to the prey abundance. Species 2 and 3 were the main prey of species 5, while species 1 and 4, which have lower abundances, form only a small part of the diet of "piscivorous" phenotypes of species 5. The proportion of fish in the diet keept increasing with size, albeit at a lower rate at low κ. This means that in Fig.3.8f there was enough food available to produce more fish that will become prey of species 5; whereas in food shortage situations (Fig.3.8d),

species 5 had to rely more on the background resource (which spans sizes from 10^{-10} to 1g spanning sizes, broadly representing sizes from picophytoplankton to macrozooplankton). This dependence on the resource spectrum explains why the higher PPMR values evolved in low κ settings found in Fig.3.2. On the other hand, "piscivores" with low PPMRs that are feeding closer to their body size showed a "piscivore" diet starting at smaller sizes ($10g$, Fig.3.8f) and were no longer directly reliant on the resource spectrum from $10^2 g$. Some cannibalism was observed at the largest sizes, making up to 40% of the diet at $10^4 g$.

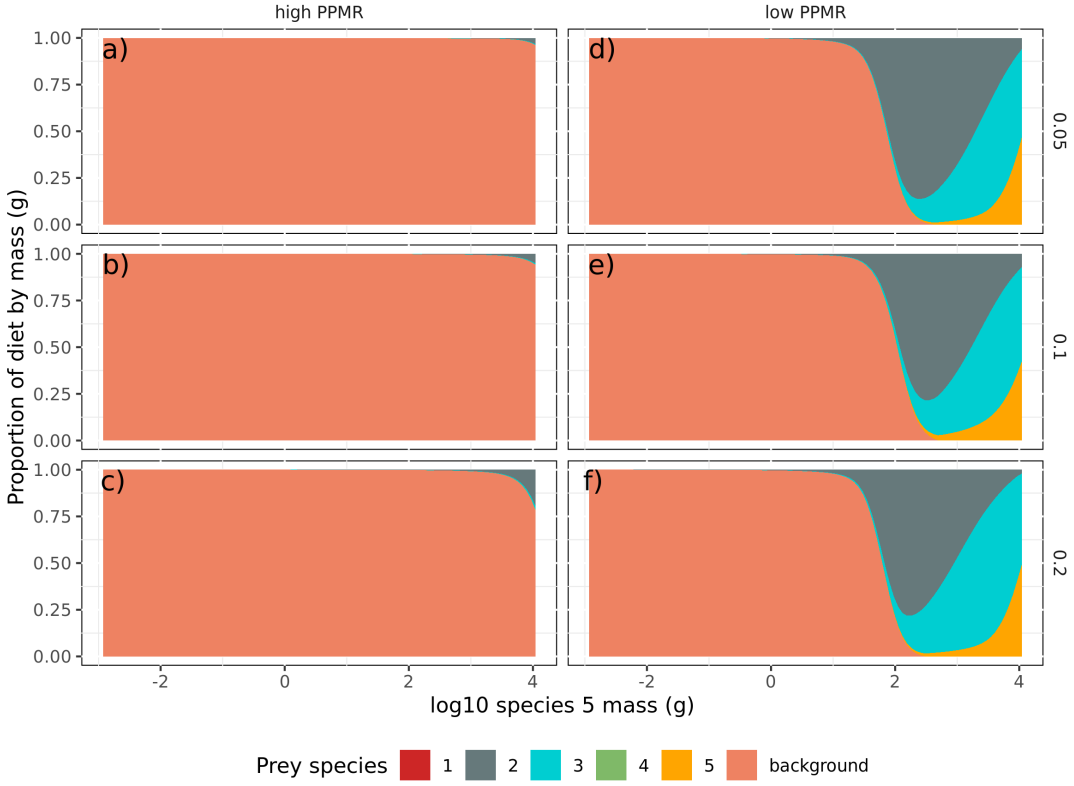


FIGURE 3.8: Diet composition of the largest species in the community per kappa from representative simulations. The diet is divided between high PPMR (a,b,c) and low PPMR (d,e,f) to make the distinction between respectively the "planktivory" and "piscivory" strategy from Fig.3.3. Species are ordered from smallest to largest. The diets of the other species can be found in appendix C (Fig.S.1).

3.5 Discussion

This study showed that 5 modelled interacting species of different asymptotic sizes adapted different PPMR strategies, depending on levels of resource availability. Species' PPMR generally increased with asymptotic size but, across all species, shifted to lower values when resource availability increased. The key exception was the largest species, which developed two feeding strategies – adopting higher PPMRs as food becomes scarcer. These PPMR adaptations affected transfer efficiencies but led to a stabilisation of the slope of the community size spectrum across all resource levels. I discuss the ecological significance and implications of these findings below.

Predator-prey mass ratios have been widely studied in ecology for informing food web structure (Elton, 1927; Cohen et al., 2003), interaction strengths (Emmerson and Raffaelli, 2004), and prey size selection in dynamic size spectrum and food web models that in turn has been shown greatly influence stability (Law et al., 2009; Brose, 2010). Typically predator-prey mass ratios used in unstructured food web models and trait-based or multispecies size-structured models are assumed to be fixed parameters, either for all species in a food web (Andersen and Beyer, 2006) or as a means of parameterising species differences (Blanchard et al., 2014). In real food webs, large variation in predator-prey mass, both within and across species, has been observed along with predator body size vs. prey body size relationships that underpin them (Brose et al., 2006a; Barnes et al., 2010; Naisbit et al., 2011; Brose et al., 2019). Here, we showed that when preferred mean PPMR is allowed to vary through natural selection a wide range of size selective strategies emerges and coexists within and across species. These strategies span the wide range of PPMR observed for fish (Barnes et al., 2010), but perhaps the most notable is the emergence of the highest PPMR for the largest species in the model.

The emergence of large PPMR for larger species was consistent with variation in wild populations (McClain et al., 2015; Vermeij, 2016) and this pattern has been used as an example of how size spectrum models (which often assume a fixed PPMR of 100) breakdown for large animals that feed on much smaller prey (e.g. baleen whales feeding on krill, Pawar et al. 2019). These patterns emerged from our size -spectrum model when PPMR is allowed to evolve. More specifically, median PPMR increased with species asymptotic sizes, across different levels of

resource availability, and only at high resource availability was bimodal, with some predator phenotypes feeding on relatively larger prey for their body size. Previous empirical studies have shown that mean PPMR increases with predator body size, when species average body sizes are used (Brose et al., 2006a; Riede et al., 2011; Brose et al., 2019) or when individual predator-prey body sizes are used (Barnes et al., 2010; Nakazawa et al., 2011, 2013). Trade-offs which yielded low assimilation efficiency on average did not allow piscivory strategies to emerge for the largest species. It appears that piscivory cannot evolve under these trade-offs because intermediate values of PPMR ($100 - 1000$) are not viable and stopped the largest species to evolve towards lower PPMR that would have had high assimilation efficiency as with the other tested trade-offs. In such case, the largest species feeding exclusively on the background spectrum led to their out-competition for food and the extinction of the smallest species.

There are several ways in which our measures of PPMR need to be carefully interpreted with respect to the empirical literature. Empirical measures of species- and individual-level PPMR (empirical data) have all been based on dietary data and therefore show "realised" PPMR, which is influenced by the prey abundance in the environment as well as underlying consumer prey size preferences (Tsai et al., 2016). Individual log prey body size vs log predator body size relationships can produce high "realised" PPMRs at large body sizes through the intercepts of these relationships when slopes are not equal to one, (Naisbit et al., 2011). We allowed mean "preferred" PPMR to evolve through time such that new phenotypes would have new trait-values but this PPMR remained a fixed ratio throughout their lifetime (equivalent to a slope of 1 on a log predator vs log prey size plot). We also had prey size variation around this value because it forms part of a lognormal prey-size selection kernel that has both a mean "preferred" PPMR (β, the evolving trait) and a standard deviation (σ) to enable a range of suitability sized prey. We used the correction of Hartvig et al. (2011) to adjust these estimates for comparison with data. In their model, Hartvig et al. (2011) predicted that "realised" community-level PPMR increases with individual predator size, even when a fixed "preferred" mean PPMR was assumed, suggesting that the assumption of fixed "preferred" PPMR might not be problematic. This was further supported by Tsai et al. (2016) who corroborated these findings using empirical data.

However, for some taxa prey size does not increase with predator size according to a fixed ratio throughout life. For example, work on stable isotopes shows that some organisms continue to feed at low trophic levels and body sizes even when they themselves grow larger (herbivores, detritivores, planktivores) (Maxwell and Jennings, 2006). This could be more appropriately represented by a lower and upper prey sizes limits (Maury, 2010) or through feeding kernel that allows PPMR to vary with predator or prey body sizes (Canales et al., 2015; Heneghan et al., 2016). Additionally, the parameter controlling the width of the feeding kernel (σ) was assumed fixed, keeping the feeding kernel shape constant, as we chose to focus on PPMR which has a greater range of variations. While σ does have an effect on size spectrum model stability (wider feeding kernel is more stable, Law et al. 2009; Blanchard et al. 2011), the typical range of empirical σ values is much narrower than PPMR. To our knowledge there is no empirical evidence of a trade-off between PPMR and σ (Barnes et al., 2010) but this could be due to the fact that there has been much less focus this parameter compare to PPMR. Furthermore, we chose to link PPMR to assimilation efficiency as PPMR is the focal trait of the study but there are other trade-offs possible around assimilation efficiency, particularly body size, which could be explored in further studies. Finally, the model did not take into account other traits than can affect size-dependent prey success that would introduce even greater variation of prey size selection into this model, such as habitat dimensionality (Pawar et al., 2019), predator search speed with body size (Hirt et al., 2017) or even social pack-hunting strategy (Nakazawa et al., 2013) that can facilitate predator acquisition of prey larger than themselves. These types of processes could alter the emergent relationships between PPMR and asymptotic size that we found, as ultimately small and large individuals all adopt the same feeding modes in the model.

Importantly, PPMR was also shown to decrease with increasing resource availability. An important result of Brose et al. (2019) is that predator traits govern substantial variation in realised PPMR but here we showed that simply varying resource availability has a large effect on both preferred and realised PPMR. Resource availability has a bottom-up effect on the food-web therefore predator traits and their top-down effects are not the only determinant of PPMR. Since resource availability greatly varies between marine ecosystem types (Barnes et al., 2010) this

effect can have huge impact on the emergence of predator diets which can be further complicated by organisms migrating through different ecosystem types or habitats to find food (Pawar et al., 2019).

The flexibility imparted through evolving and coexisting PPMR strategies led to energy pathways that ultimately acted to stabilise community and ecosystem structure and function under different resource levels. Even with different β_r between scenarios of varying κ, the resulting size spectrum slope were similar (Fig.3.7, b) and were consistent with unfished spectrum slopes (-2, Andersen et al. 2008). In the case of $\kappa = 0.05$ a slightly flatter slope emerged rather than the steeper consumer size spectrum slopes typically found under lower resource levels in the absence of evolving traits (Blanchard et al., 2009). We expected that the size spectrum would have become steeper with decreasing resource availability but the inverse occurred. This suggests that with constraints on food, the different species adapt through their PPMR to maintain a size spectrum slope. Allowing the PPMR to evolve freely allowed large species to feed directly at the start of the size spectrum (small sizes), increasing the trophic transfer efficiency which results in lower losses of energy (abundance and biomass) up the size spectrum. However, transfer efficiencies we found should be interpreted with caution as the highest is 0.5 for $\kappa = 0.2$ (corresponding to mean realised community PPMR, averaged across species and average community size spectrum slope). Transfer efficiency should decrease with trophic level (Barnes et al., 2010) and therefore decrease with PPMR, which is not what we find. Low β_r implies that individuals feed closer to their body size and therefore the food chain will have more steps between plankton and apex predators, leading to longer food chains and more stable ecosystems (Jennings and Warr, 2003). In this case transfer efficiency did not show an apparent link with PPMR (and by extension food chain length) although we used an unweighted community mean PPMR in these calculations and an approximate community size spectrum slopes, in keeping with Barnes et al. (2010). However, in an empirical study, (Reum et al., 2019) showed consistent dome-shaped patterns in biomass weighted PPMRs with respect to predator body size. Moreover, they suggested that weighting community PPMR by biomass would be more appropriate for informing overall energy flow.

Feeding with a high PPMR way down the food chain usually destabilises modelled size spectra

(Blanchard et al., 2008; Law et al., 2009). However, as the resource spectrum in our model did not have seasonality and was constantly replenished, it could counterbalance this instability by providing a constant food source for larger predators and thus allowed stable communities and persistence of large predators even in reduced resource availability, comparable to the emergence of high PPMR apex predator in Woodson et al. (2018). Ochiai et al. (2012) showed in another study on food web structure that with a simple evolutionary model, the ratios among basal species (prey), intermediate species (predators and prey species) and top species (predators) within the modelled food-web would evolve close to what is found in natural system (0.19 : 0.52 : 0.29). In this study, whether the emergent patterns of PPMR and size spectra were the consequences of self-organisation, requires further work and could be further used to develop understanding on how food-web structure emerges through evolutionary history.

The simulated food web in this study yielded realistic networks adaptations, implying that modelling eco-evolutionary feedbacks within the size-structured framework can help understand how predatory interactions and other factors such as resource availability determines food-webs structure (Segar et al., 2020).

3.6 Tables

TABLE 3.1: Model equations for each species' ecological dynamics. Subscripts for each species are not included in the equations below for readability. These dynamics also hold for each phenotype (nested within each species) once they have entered the size spectrum. Equation numbers reference the processes described in the main text. $N(m)$ is the density at size driven by: $g(m)$ which is the feeding dependent growth rate at size and $\mu(m)$ which is the mortality at size, the latter is comprised of several mortality terms below. All parameter values and definitions are provided in Table 3.2 or the main text.

Equation	Description	
Species population dynamics	$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$	(E1)
Background resource dynamics	$\frac{\partial N_R(m,t)}{\partial t} = r_0 m^{p-1}\left[\kappa_R m^{-\lambda} - N_R(m,t)\right] - \mu_p(m)N_R(m,t)$	(E2)
Prey size selection by size m predator	$\phi(m, m_p) = exp\left[\frac{-(ln(m/(\beta m_p)))^2}{2\sigma^2}\right]$	(E3)
Encountered food by size m predator across all sizes (mp) of species j prey	$E(m) = \gamma m^q \int \left(N_R(m_p) + \sum_j \theta_j N(m_p)\right)\phi(m, m_p) m_p \mathrm{d}m_p$	(E4)
Feeding level	$f(m) = \frac{E(m)}{E(m) + hm^n}$	(E5)
Somatic growth	$g(m) = (\alpha f(m) h m^n - k_s m^p)(1 - \psi(m))$	(E6)
Energy allocation towards reproduction	$\psi(m) = \left[1 + \left(\frac{m}{m^*}\right)^{-u}\right]^{-1}\left(\frac{m}{M}\right)^{1-n}$	(E7)
Reproduction	$R_p = \frac{\epsilon}{2m_0}\int N(m)(\alpha f(m) h m^n - k_s m^p)\psi(m)\mathrm{d}m$	(E8)

Recruitment	$$R = R_{max}\frac{R_p}{R_p + R_{max}}$$	(E9)
Predation mortality on size mp prey inflicted by all sizes (m) of species j predators	$$\mu_p(m_p) = \sum_j \int \phi(m, m_p)(1 - f_j(m))\gamma_j m^q \theta_j N_j(m)\mathrm{d}m$$	(E10)
Senescence mortality	$$\mu_{se} = \begin{cases} se_{min} + (se_{max} - se_{min})e^{-\frac{M}{m}}, & \text{if } m > m^* \\ 0, & \text{otherwise} \end{cases}$$	(E11)
Starvation mortality	$$\mu_{st} = \begin{cases} st_r m\left(k_s m^p - \alpha f(m) h m^n\right), & \text{if } k_s m^p > \alpha f(m) h m^n \\ 0, & \text{otherwise} \end{cases}$$	(E12)
Background mortality	$$\mu_b = \mu_0 M^{n-1}$$	(E13)
Fishing mortality	$$\mu_f = \begin{cases} 0.8, & \text{if } m >= m^* \\ 0, & \text{otherwise} \end{cases}$$	(E14)

TABLE 3.2: Parameters table. M is noted "variable" as it is species specific (values in Table 3.3). β starts at 1000 for all species but will evolve during the simulations. κ has a value of 0.05, 0.1 or 0.2 for each scenarios. Parameters values are taken from Hartvig et al. (2011). The value from γ was calculated from: $\gamma = h\frac{f_0}{\sqrt{(2\pi)}\sigma\beta^{\lambda-2}e^{((\lambda-2)^2\sigma^2/2)}\kappa(1-f_0)}$ (Hartvig et al., 2011). Initial values for the abundance density $N(m)$ of each species at $t = 0$ were based on the equilibrium equation: $N = \frac{\kappa}{1000}M^{(2n-q-2+0.35)}m^{(-n-0.35)}$ provided in Andersen and Beyer (2006).

Symbol	Value	Units	Parameter
Individual growth			
M	variable	g	Asymptotic size
η	0.25	-	ratio between M and m^*
m^*	ηM	g	Maturation size
f_0	0.5	-	Initial feeding level
γ	538	$g^{-q}m^3yr^{-1}$	Factor for search volume
α	0.6	-	Assimilation efficiency
h	85	$g^{1-n}year^{-1}$	Maximum food intake
n	0.75	-	Exponent for max. food intake
p	0.75	-	Exponent for standard metabolism
ks	4	-	Factor for standard metabolism
β	100	-	Preferred predator-prey mass ratio
σ	1	-	Width of the feeding kernel
q	0.8	-	Exponent of search volume
Reproduction			
m_0	0.1	mg	Offspring mass
ϵ	1	-	Efficiency of offspring production
u	7	-	Width of maturation transition
Mortality			
ξ	0.1	-	Fraction of energy reserves
μ_0	2	$g^{1-n}year^{-1}$	Background mortality
se_{max}	1	$g^{1-n}year^{-1}$	Upper limit for senescence mortality
se_{min}	0.1	$g^{1-n}year^{-1}$	Lower limit for senescence mortality
st_r	0.1	$year^{-1}$	Starvation mortality cost
θ	0.5	-	Interaction matrix species-specific value
Resource spectrum			
κ	variable	$g^{\lambda-1}m^{-3}$	Magnitude of resource spectrum
λ	$2-n+q$	-	Slope of resource spectrum
r_0	5	$g^{1-p}year^{-1}$	Regeneration rate of resources
m_{cut}	1	g	Upper limit of resources spectrum
Evolution			
χ	0.003	-	Phenotype's introduction probability
Ω	10^{-30}	$individual/m^3$	Extinction threshold
	5%	-	Fraction of initial phenotype's abundance
ζ	$+-20\%$	-	Magnitude of trait evolution

TABLE 3.3: Initial maturation, asymptotic size and R_{max} of the species.

Species	Maturation size (g)	Asymptotic size (g)	R_{max}
1	2.5	10	0.49208
2	14	56	0.08167
3	79	316	0.01312
4	445	1778	0.00210
5	25000	100000	0.00034

Chapter 4

Generalist thermal strategies emerge in response to rapid warming in a size structured model

4.1 Summary

The impact of climate change on natural systems is driving rapid ecological and evolutionary changes. Global warming is causing gradual increases in temperature, as well as temperature anomalies and extremes. Many fish species exhibit ranges of thermal performance. Narrow ranges are thought to have evolved under relatively stable temperature conditions, whereas wider ranges represent a generalist thermal strategy. Yet, it is unclear which of these two strategies are beneficial under different projected warming climate scenarios and how species interactions might affect the emergence of thermal performance traits. Here we used a variant of a trait-based size spectrum model with adaptive (selection driven) trait dynamics, where new phenotypes are introduced randomly, and their invasion success is tracked through time. We used the model to explore evolutionary changes in fish thermal performance (thermal optimum and range) and changes in the community structure in response to past and projected sea surface temperatures. We found that the rapidly increasing temperatures and increased frequency of heat waves select for generalist thermal strategies, resulting in up to 30% change in species' thermal optima. The existing phenotypic diversity in populations allowed for rapid responses to selection, but strong

selection pressures quickly led to a rapid reduction of fitness of some phenotypes and a collapse in overall phenotypic diversity. These changes were followed by a decrease in community biomass and an increase in the variability of and steepening in size spectrum slope.

Keywords

ecosystem structure, coexistence, evolution, food webs, trait-based size spectrum model, temperature scaling, global warming

4.2 Introduction

Global warming affects every organism on Earth. Increasing temperatures are changing the ocean's physical and chemical composition, the biological processes of primary production (Sarmiento et al., 2004), and thus entire food webs and ecosystems (Brander, 2007). Many experimental and observational studies have demonstrated the multifaceted effects of warming on marine organisms (Jochum et al., 2012; Twomey et al., 2012), with the increased frequency of marine heatwaves (Holbrook et al., 2019; Bindoff et al., 2019) leading to devastating impacts on marine biodiversity and ecosystems (Garrabou et al., 2009; Wernberg et al., 2013; Pearce and Feng, 2013).

How changes in physiological processes scale up to changes at population, community and ecosystem levels is still not well understood (Sutherland et al., 2013). While metabolism generally increases with temperature (Brown et al., 2004), other processes (such as food intake or maturation) often exhibit optima whereby performance decreases past an intermediate temperature threshold (Padfield et al., 2016). Theory predicts that growth efficiency decreases with increasing temperature (Berrigan and Charnov, 1994) but not all ectotherms follow this pattern and the underlying mechanisms remain debated (Ashton, 2001). One of the key questions in this debate is the role of body size in thermal performance and adaptation (Angilletta and Dunham, 2003). If energy acquisition and consumption scale differently with body size and with temperature, the thermal optimum for growth rate and other physiological processes will also

change with increasing body size (Bjornsson, 2001; Morita et al., 2010). The population and community consequences of temperature changes will therefore depend on the size composition of populations (Kingsolver and Huey, 2008; Ohlberger et al., 2012; Verberk and Atkinson, 2013).

Communities are also influenced by food web interactions, which are similarly dependent on the sizes of predators and prey (Jennings et al., 2001; Cohen et al., 2003; Woodward et al., 2010). Therefore, to model temperature effects on whole communities we need to consider the interplay of body size and physiological processes in a multi-species size-based context (Ohlberger et al., 2012; Lindmark et al., 2018b).

Most organismal studies on the effects of temperature focus on direct physiological effects rather than the adaptation of thermal performance. There is a debate regarding whether there is clear evidence of organisms acclimating or adapting to climate change (Crozier and Hutchings, 2014; Stoks et al., 2014) as it is hard to prove adaptation using correlative methods, any adaptation is occurring against a background of natural variability in global warming, and there are a number of different factors influencing adaptation (but see Kosaka et al. (2019) who show bacteria do demonstrate thermal adaptation). Plasticity can also add to the effects of adaptation (Kingsolver and Buckley, 2017) but has been shown to have limited effect on the thermotolerance of marine ectotherms (Gunderson and Stillman, 2015). Due to these different responses to temperature changes and their impact on thermal performance, it is challenging to predict how different organisms will react and adapt to global warming (Hoffmann and Sgrò, 2011; Merilä and Hendry, 2014; Donelson et al., 2019).

Some species consist of individuals that are temperature generalists, performing reasonably well at a wide range of temperatures (e.g. intertidal fish, Somero 2002. In contrast, specialists perform best at a specific temperature (e.g. subzero fish, Wilson et al. 2002). This thermal adaptation could explain the variety of thermal performances observed within and among species (climate variability hypothesis Donelson et al. 2019). A specialist–generalist trade-off happens when the temperature performance breadth causes a decrease in the maximal thermal performance (Angilletta, 2009) (i.e. an improvement in performance at low temperature requires a decrement

in performance at high temperature, and vice versa Levins 1968; Palaima 2007). A specialist for low or high temperature will have a higher maximum fitness than a generalist albeit over a small temperature range. Thus, these trade-offs constrain the variability in thermal performance adaptation due to their constraints on evolution (Angilletta, 2009).

Size spectrum models are physiologically structured multi-species models and are therefore very well suited to study temperature effects on size, population and community dynamics. These models have been successfully applied to study changes in individual body size distributions of communities and ecosystems in response to human-driven changes in temperature (Blanchard et al., 2017a; Woodworth-Jefcoats et al., 2019; Lefort et al., 2015; Lotze et al., 2019). However, until now the models have not explored the importance of phenotypic diversity and evolution in the context of climate change. Such an exploration is needed, as knowledge of the adaptive capacity of populations and emergent effects on communities are of critical importance for understanding the impacts of climate change (Fraser, 2013).

In this study we used the unimodal (*sensu* Padfield et al. 2016) temperature scaling of physiological processes (bell shaped) into an eco-evolutionary size and trait-based model (Forestier et al., 2020) to investigate fish community adaptation to human-induced temperature increases and a higher frequency of heat waves. We modelled communities adapted to a relatively stable climate followed by a global warming projection of $3.5°C$ increase in temperature per a hundred years combined with increased variability in the amplitude and frequency of temperature (i.e. heat waves).

We hypothesised that a stable climate should be advantageous to temperature specialist strategies, whereas the global warming projections will be less detrimental to temperature generalists and warm-adapted organisms, able to respond to the large temporal variability in temperature. We further investigated how the rate of evolutionary change influenced modelled community dynamics via species' thermal performance adaptations under the global warming projection.

4.3 Methods

In this study we explored the eco-evolutionary feedbacks between individual thermal performance strategies defining thermal optimum and specialisation, and community structure and population dynamics. To model the eco-evolutionary dynamics of a simulated fish community we used a trait-based size spectrum model (Andersen and Pedersen, 2010; Hartvig et al., 2011), modified to allow adaptive changes in trait values (Forestier et al. 2020, mizerEvolution). We allowed for adaptation in two traits defining thermal performance of individuals' net energy intake rates. Below we describe the model in four parts: 1) an ecological component, which defines intra- and inter-specific interactions that act as selective forces influencing survival and community dynamics (i.e. as in the basic "mizer" package, Scott et al. 2014), 2) a temperature component where environmental temperature acts on organism's physiology, 3) an evolutionary component that generates random new trait combinations introduced to the community at each time step ("MizerEvolution") and selected upon through ecological interactions and 4) a climate warming simulation design using sea surface temperature outputs of a general circulation model for a marine warming and heatwave hotspot: southeast Australia.

4.3.1 Ecological component

Size spectrum models are physiologically structured models that track the density of individuals at size through time (Andersen, 2019). The model framework allowed for the coexistence of several species that differ by their asymptotic size. All physiological processes were food-dependent (i.e., growth, mortality, reproduction) and dependent on size-based interactions. Processes and interactions were computed at every time step, the model therefore assumed continuous reproduction. Species' population dynamics were obtained by solving the mass conservation equation (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$$

where m is the species mass, and individual growth $g(m)$ and mortality $\mu(m)$ were determined

by predation on/from other individuals and a background resource spectrum modelled using a semi-chemostat growth assumption (Table 4.1, E2).

There were two sources of food in the model: the fish community spectrum made up of the different species and the background resource spectrum, which here was assumed to extend between the size of 10^{-10} to 1g (bacteria to zooplankton) (Table 4.2). In the trait-based model used here, feeding interactions depended entirely on body size (there is no diet preference across species), so all fish individuals could simultaneously be predator and prey, depending on their sizes.

Mortality had four different sources. An emergent predation mortality, senescence mortality (Table 4.1, E12), starvation mortality (Table 4.1, E13) and a constant background mortality where larger species were assumed to have lower background mortality (Table 4.1, E14). Predation mortality constituted the major sources of mortality in the system. Further details on the ecological components and assumptions used are available in chapter 2, and on the "mizer" website (https://sizespectrum.org/mizer/).

4.3.2 Temperature component

In our model we assumed that temperature affects the net food intake, through temperature effects on search rate, handling time and metabolism. We assumed that food acquisition (search rate and handling time) has steeper temperature scaling than metabolism (Lindmark et al., 2018a), which means that net energy intake will increase with increasing temperatures up to an optimum, at which point it will start to decrease (Asbury and Angilletta Jr., 2010; Dell et al., 2011)(Fig.4.1). Higher net energy intake increased reproductive output and therefore led to a higher fitness.

We used a unimodal temperature scaling function (r) from Schoolfield et al. (1981) modified to include a reference temperature (T_{ref}) at which the temperature scaling of the rate equals one (Gårdmark et al., prep). This function scaled the net food intake up or down depending on the reference (T_{ref} and ambient temperature (T) ($r(T, T_{ref})$ term in E3, Table 4.1 and Fig.4.1). $r(T, T_{ref})$sacles up/down the search volume (γ, Table 4.2) in the model, affecting the net food intake and predation mortality. In cases where the net energy intake went down, it meant that

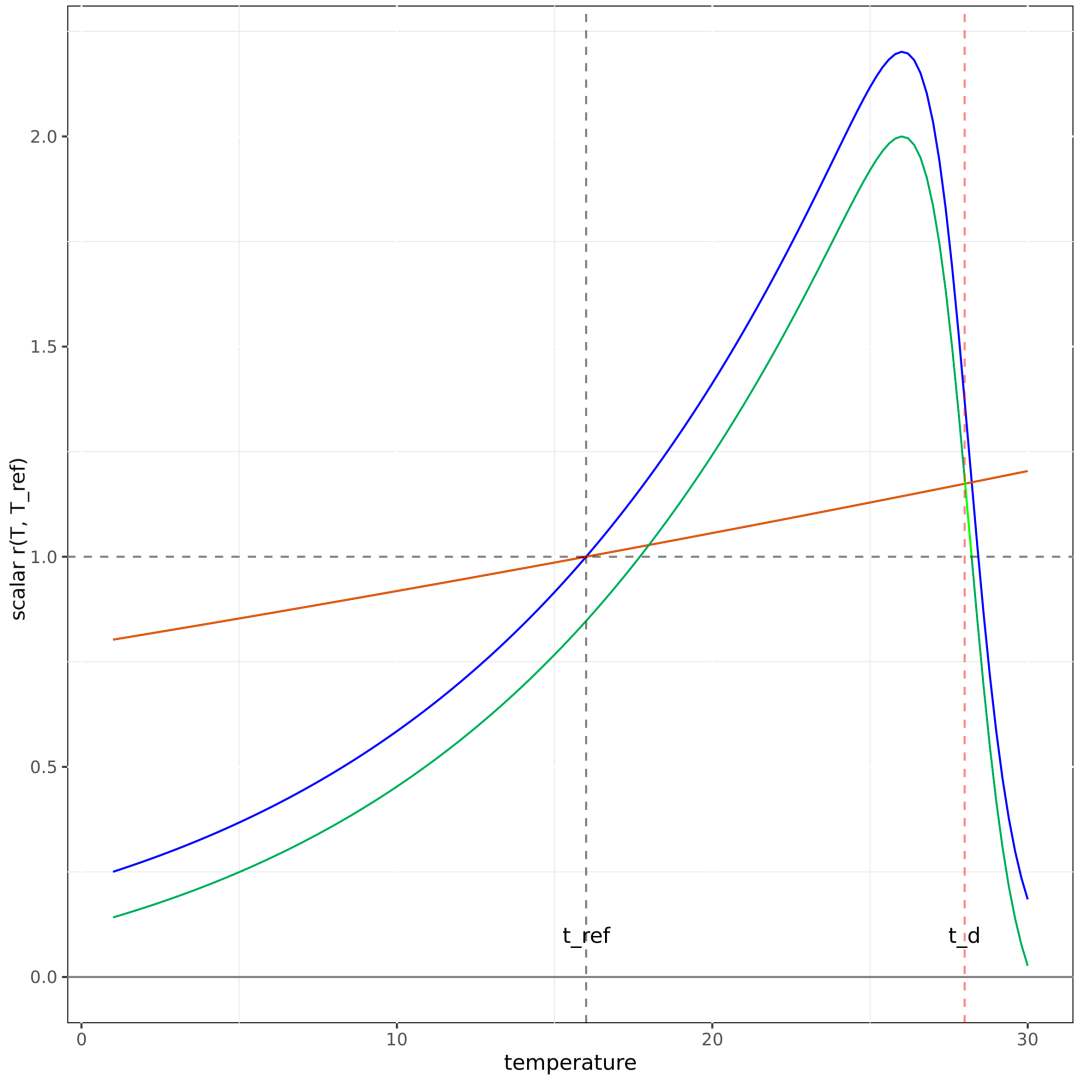


FIGURE 4.1: Example of scaling of metabolism (orange) and food intake (blue) across a temperature gradient, yielding a relative net energy intake (green). The scalar multiplies the rates (e.g. metabolism or food intake). Metabolism and food intake are scaled independently of each other, the resulting net energy intake is the difference between food intake and metabolism after the temperature scalar has taken effect. The net energy intake is not a scalar but is shown here to illustrate how scaling metabolism and food intake affects organisms.

the food intake could not compensate for increasing metabolism costs. The scalar values were obtained from the temperature performance curve which has a unimodal shape with a maximum scalar value at the temperature optimum and scalar value of 1 at the reference temperature (T_{ref})

$$r(T, T_{ref}) = e^{\frac{-E_A}{k}(\frac{1}{T}-\frac{1}{T_{ref}})}.(1+e^{\frac{-E_D}{k}(\frac{1}{T}-\frac{1}{T_D})})^{-1}.(1+e^{\frac{-E_D}{k}(\frac{1}{T_{ref}}-\frac{1}{T_D})})$$

where k is Boltzmann constant, E_A is the activation cost, E_D is deactivation cost, T is the temperature, T_{ref} is the temperature reference and T_D is the temperature at which the rate has declined to half. In this equation, the traits E_A and E_D determined the steepness of rate increase and decrease, whereas the traits T_{ref} and T_D determined the position of the optimum compared to the environmental temperature T (Fig.4.2).

To reduce the number of independent parameters in the evolutionary model we linked some parameters in the temperature response equation (E3) to describe two temperature response traits (Fig.4.2). The first trait determined the width and the height of the curve (GS, Fig.4.2a), which created a temperature generalist/specialist trade-off where a higher performance at the optimum temperature came with a narrower range of performance around this maximum and vice versa (Angilletta, 2009). The trade-off was obtained by linking activation and deactivation rate parameters (E_A and E_D), controlling the slope of the performance curve around the optimum. We explored a range of options to link E_A and E_D (Fig.S.1) to find a combination that allowed the desired performance curve properties: a) specialists should have a narrower and higher curve than generalists, b) the difference between maximum performance between generalists and specialists should not exceed a 1.5 ratio. This meant that, for example, a highly specialised species with ($GS = 11$ and $\sim 1°C$ window of good performance) had a maximum net intake scalar of 3 at their optimum temperature, whereas a generalist species ($GS = 3$ giving $\sim 5°C$ wide window of good performance) only had a maximum net intake scalar of 2. These properties were achieved using the relationship between E_A and E_D as

$$GS = E_D | E_A = -0.009.E_D + 1$$

Other combinations of E_A and E_D gave emergent performance curves that did not fit with the assumption that a specialist have a narrower performance curve than generalists (Fig.S.1).

The second trait determined the value of the optimum temperature (TO, Fig.4.2b). To model this trait, we linked parameters T_{ref} and T_D and assumed that net intake and therefore reproductive output and overall fitness increased with increasing temperatures. This assumption

follows the "hotter is better" paradigm, meaning that species living (and adapted to) warmer environment have overall greater performance than species living in colder environment (Huey and Kingsolver, 1989; Kingsolver and Huey, 2008; Angilletta, 2009; Angilletta et al., 2010). To link the T_{ref} and T_D traits we aimed to find a combination of parameters that increased net intake at higher temperatures without giving an overwhelming advantage to warm temperature adaptations; as with the GS trait we assumed that performance at warm temperatures can be up to 1.5 higher than at cold temperatures (Fig.4.2b). This was achieved by assuming that

$$TO = T_D | T_{ref} = T_D - (5 + 0.25.T_D)$$

producing a TO trait that can evolve along the temperature gradient (Fig.4.2b). This set-up of linked parameters decreased the number of independently evolving parameters from 4 to 2 (GS and TO). Evolutionary dynamics of these traits are described in the next section.

Taking into account the changes described above (i.e. E_D and E_A combined in to GS and T_D and T_{ref} combined into TO), E3 can be rewritten as:

$$r(T) = e^{\frac{0.009.GS+1}{k}(\frac{1}{T} - \frac{1}{TO-(5+0.25.TO)})}.(1 + e^{\frac{-GS}{k}(\frac{1}{T} - \frac{1}{TO})})^{-1}.(1 + e^{\frac{-GS}{k}(\frac{1}{TO-(5+0.25.TO)} - \frac{1}{TO})})$$

4.3.3 Evolutionary Component

The evolutionary component of the MizerEvo modification is described in detail in Chapter 2 and Forestier et al. (2020). Briefly, at every model time-step (i.e. 10 times per year) there was a probability χ (Table 4.2) of a new phenotype being introduced in the simulation. An existing phenotype ("parent") was selected randomly from the existing phenotype pool and gave rise to a new phenotype. This new phenotype was an exact copy of its parent except for the two thermal performance traits which were assigned a slightly different trait value. The new trait values were taken randomly from a normal distribution centred on the parent's traits value with a standard deviation (or variance) of 0.2 (ζ, Table4.2), leading to an average change per species of 4.5% per

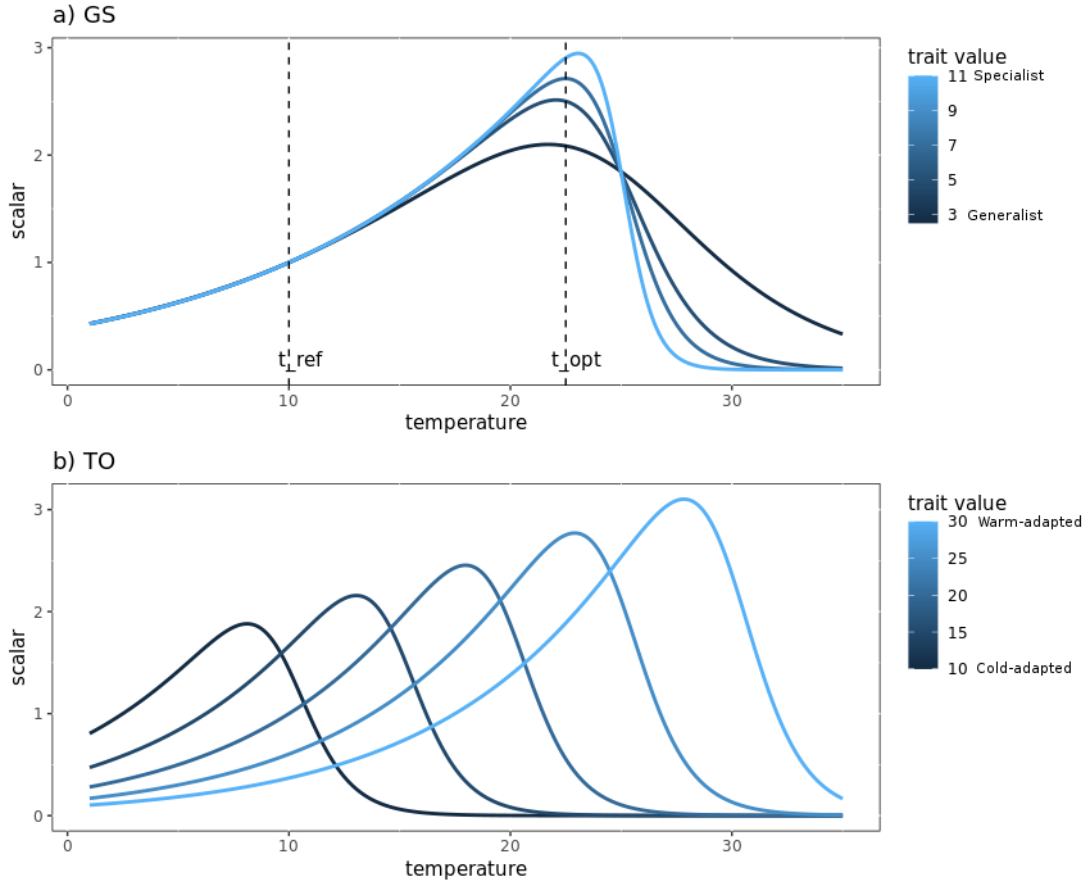


FIGURE 4.2: Temperature performance curves, over a range of temperature values defining generalist-specialist trait gradient (GS, a panel), and temperature optimum trait gradient (TO, b panel). Higher GS values indicate increasing thermal specialisation, and higher TO values show increasing optimum temperatures. At T_{ref} the scalar will be 1, at T_{opt} the scalar will be at the maximum. T_{ref} and T_{opt} values for all GS traits are the same (shown with dashed vertical lines). The resulting scalar multiplies the food intake rate.

year. We assumed that both traits were in complete linkage equilibrium (i.e. they are inherited independently).

All phenotypes within species competed with each other (intra-specific competition). The least fit phenotypes went extinct, simulating natural selection in the ecosystem. A stock recruitment relationship was used to implement early life density dependence, which places a maximum value on their realised spawn output (Andersen et al., 2016a). Phenotypes within one species shared this maximum output among themselves, which is scaled on their spawn output (i.e., a phenotype with a high spawn output will have more recruits with its traits than a phenotype with a low spawn output).

To assess sensitivity of model outcomes to our assumptions about mutation rate (rate of new phenotype appearance), we ran simulations with the probability χ values ranging from 0.001 to 0.01.

In all simulations we used a model composed of 9 species with asymptotic sizes equally spread over a logarithmic scale between 10 to $10^5 g$. All species were identical except for the two studied traits and their asymptotic size. The initial abundance of each species was determined based on the equilibrium conditions (Andersen and Beyer, 2006), which uses feeding and carrying capacity parameters to estimate biomass at equilibrium. Species abundance was then divided randomly among 20 initial phenotypes per species. These phenotypes were generated using the same method described above except using a ζ three times higher to create a wide phenotypic diversity at the start of the simulation. This meant that the initial phenotype abundances and phenotype identity across stochastic realisations were different. 70 simulation replicates were used in the results.

To assess the effects of adaptation to the climate scenarios on functional diversity and community dynamics, we calculated changes in the number of phenotypes per species, the total biomass of the community and the community size spectrum slope through time, for each stochastic replication.

4.3.4 Climate forcing design

To force our model with hypothetical but broadly realistic temperature changes, we needed to characterise a stable and climate change period that were broadly consistent with climate model projections, and which captured both long-term trends and variability. To characterise our stable and climate change simulations we extracted and analysed Earth System Model (ESM) sea temperatures from CMIP5 (https://pcmdi.llnl.gov/?cmip5/), specifically the IPSL-CM5A-LR model outputs for the most extreme (rcp8.5) emissions scenario. We extracted monthly outputs of depth integrated temperatures for historical (1970–2005) and future (2006–2100) projections and spatially averaged these for grid cells within the southeastern Australia Large

Marine Ecosystem (https://www.sciencebase.gov/catalog/item/55c77722e4b08400b1fd8244), a recognised climate change hot-spot (Pecl et al., 2014).

First, we allowed the phenotypic diversity to build up using simulated temperature data mimicking a stable period without climate change. The first climate phase was an initialisation phase where the communities initialised by the model were projected for 3000 years of simulation time. To approximate a stable temperatures which could be used as MizeEvo input data we analysed the time series of temperature during the historical period 1970-2000 and estimated the key parameters below to reconstruct a longer historical spin-up forcing, that removed the long-term trend. We simulated data instead of using the historical time-series as it gave us free choice of number of time-step per year and simulation length. The simulated time-series can be divided in three components: an annual mean temperature, a seasonal variation and a random deviation from both previous components as heatwaves, which are detailed below:

$$Temp_i = AnnualMean_i + Season_i + Heatwave_i$$

$$AnnualMean_i = 10.55$$

$$Season_i = 1.7\cos(2\pi(i + 0.25))$$

$$Heatwave_i = lognormal(\mu = 0; \sigma = 0.45) - exp((-0.45)^2)$$

where i is the absolute number of time-step forming a full seasonal cycle in 10 time-steps. Once the species had reached stable trait values, the climate was switched to the global warming simulation scenario. This global warming simulation scenario projected an increase in temperature of $3.5°C$ per 100 year, combined with the increased frequency of heatwaves. As we wanted to run the model for a period of 200 years (to be able to compute the fitness of species' cohorts until 150 years of warming), this scenario did not use data directly from the rcp8.5 projection across 2006-2100 described above, rather it was statistically informed by the projection to allow for a longer period of 200 years. The rcp8.5 scenario was approximated by incorporating: 1) an increasing temperature trend of $3.5°C$ per 100 year and 2) a temporal trend in the distribution

of heatwaves simulated by a skewed normal distribution to better mimic the gradual increase in frequency and amplitude of warmer temperature anomalies that occurred later in the IPSL model time series (Fig.4.3b).

$$Temp_i = AnnualMean_i + Season_i + Heatwave_i$$

$$AnnualMean_i = 10.55 + 0.0035i$$

$$Season_i = 1.7\cos(2\pi/(i + 0.25))$$

$$Heatwave_i = 2\phi(i)\int_{-\infty}^{\alpha i}\phi(t)dt$$

with $\phi(i) = \frac{1}{\sqrt{2\pi}}e^{-\frac{i^2}{2}}$ and i is the absolute number of time-step since the start of the global warming.

As heatwave frequency and amplitude followed the increase in temperature, their parameters followed a linear increase of the time-steps such that:

$$x_i = -0.6 - 0.0003512i$$

$$\omega = 1.01 + 0.000878i$$

$$\alpha = 2.8 + 0.001932i$$

With x_i, ω and α respectively the location, scale and shape of the skewed normal distribution.

As values were sampled from the skewed normal distribution at every time-steps to generate the climate, each simulation got a slightly different temperature forcing due to the variations of the white noise. However, the approximated temperature values captured the key trends in the IPSL-CM5A-LRmodel projections (one temperature realisation is shown in Fig.4.3).

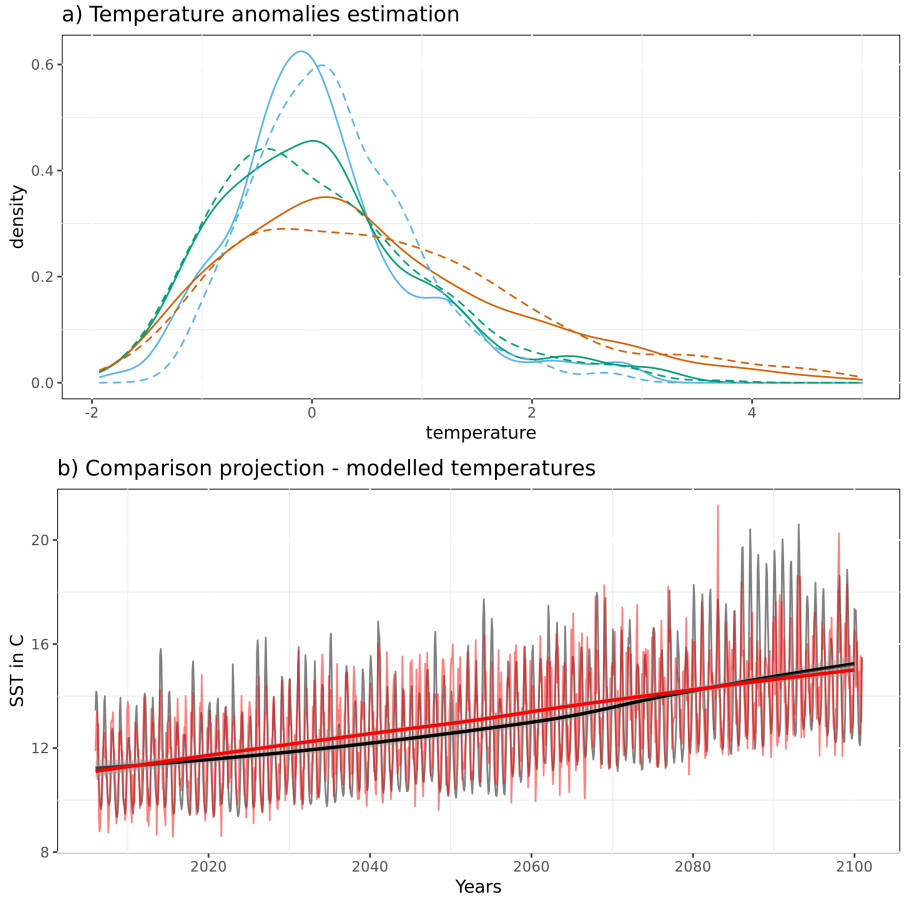


FIGURE 4.3: Construction of the heatwave for the model. a) shows shifts in the distribution of temperatures anomalies around the long-term trend from the rcp8.5 projection (after removing seasonal variation and warming trend). The right-hand tails of these distributions represent heat-wave events. The blue solid line shows the early heatwaves, followed by the green color for mid-century heatwaves and finally orange for late century heatwave when these events are more frequent. The dashed lines are the approximation of these data using a log-normal function. b) shows the resulting climate forcing encompassing the heatwaves modelled via the log-normal function combined with the long-term trend in red. The black line is the temperature time series obtained from the rcp8.5 scenario of the IPSL earth system model. Respective mean yearly trends were added as thick lines.

4.3.5 Evaluating model outputs

The eco-evolutionary dynamics and fitness values changed throughout the simulations as new phenotypes appeared, as such, the model was not necessarily expected to reach equilibrium conditions. Thus, after the 3000 years of simulations using the stable climate conditions, the rate of change in each trait value was small enough ($\sim$ 1% change per 100 year) to consider the ecosystem stable.

We assessed the modelled communities in terms of coexistence among phenotypes and evolutionary trends among traits (i.e., changing temperature adaptation strategies). The trait value of a species was the abundance weighted mean of its phenotypes. Within a species, success of the different trait combinations was assessed through the fitness landscapes, where fitness was defined as the average individual spawn output throughout the lifetime of a cohort of one phenotype within one species. This allowed us to qualitatively compare different phenotypes (and thus trait combinations) within species.

$$fitness = \frac{\int_{t_0}^{t_{max}} R_{max,i} \frac{R_{p,i}}{R_{p,i}+R_{max,i}} dt}{N_{p,i}(m_1, t_0)}$$

where $R_{p,i}$ is the energy allocated to reproduction (accounting for species specific density dependence) from E9, by phenotype p of species i, R_{max},i is the maximum recruitment value for species i and $N_{p,i}(m_1, t_0)$ is the initial abundance of phenotype p and species i in the cohort of interest.

4.4 Results

4.4.1 Thermal trait adaptations under variable temperature scenarios

During the 3000 years of stable climate conditions, thermal traits of all nine species quickly stabilised from the initial phenotype values. In the absence of a climate trend, there was no species-specific trend in temperature optimum trait (TO) (Fig.4.4a), and trait values quickly converged towards the optimum temperature for all species (average of $11.68 \pm 0.5°C$). This was slightly higher than the ambient mean temperature ($10.85°C$). More variation and difference among small and large species evolved in the trait defining the generalist / specialist strategy (GS trait, Fig.4.4c). While species had large variability around the mean, small species (1,2,3) had slightly narrower thermal performance windows on average than the larger species (7,8,9) (average of 8 ± 2.5)(Fig.S.2 compares last time step of each panel). The average number of phenotypes per species stabilised after 1000 years and remained relatively stable during the

remaining 2000 years of the stable climate simulations (Fig.4.5a). Larger species had a greater number of phenotypes than the small species (mean of 25 and 10 phenotypes respectively).

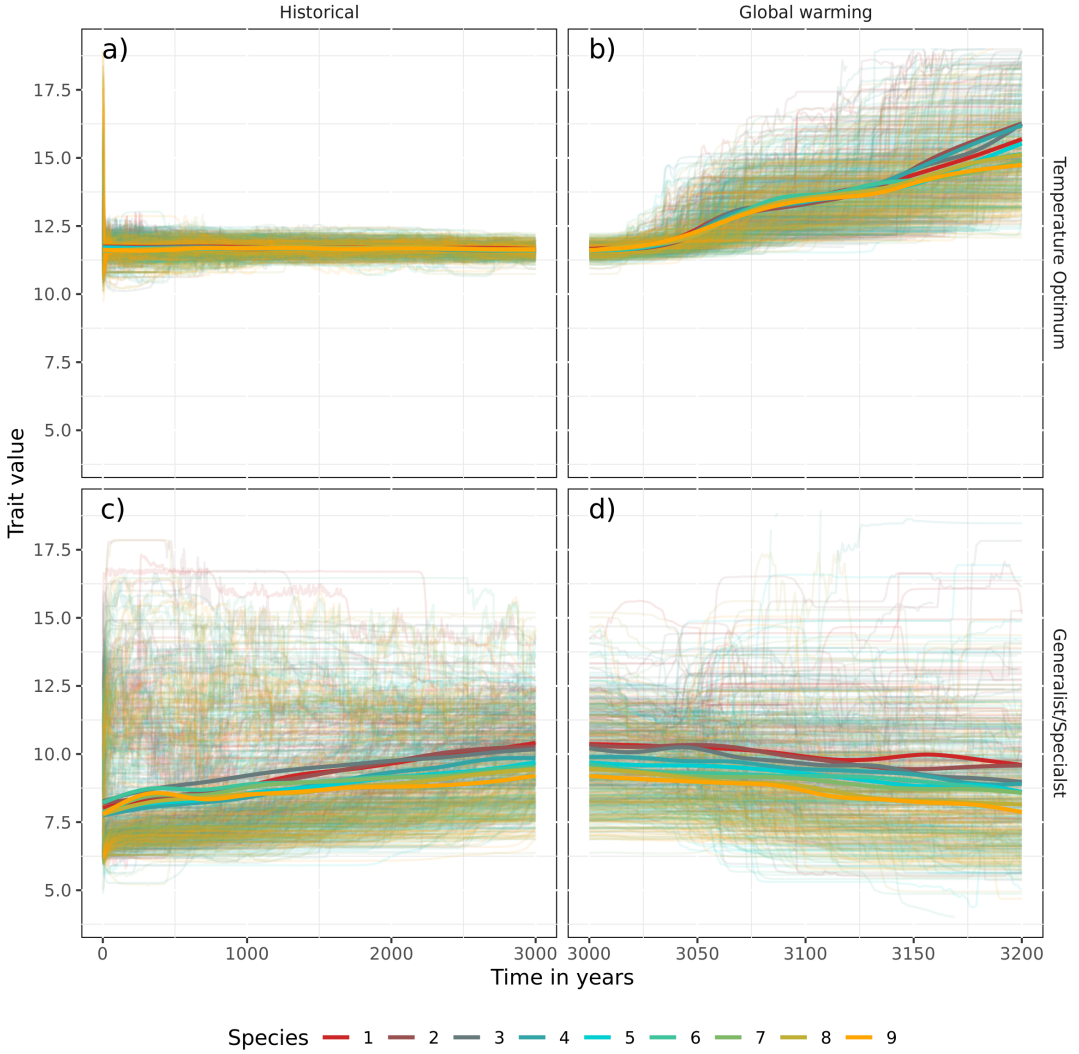


FIGURE 4.4: Mean trait value per species through time under stable climate conditions (a,c) and global warming (b,d). The solid lines are the mean values per species while the transparent ones are the values per phenotype. The trait value of optimum temperature (TO, a and b) is in degrees Celsius. The trait value for specialist-generalist behaviour (GS, c and d) represented by the width-height of the performance curve, is a unit-less gradient, with low values indicating temperature generalists and high values indicating temperature specialists. Species are ordered from smallest to largest.

As soon as global warming was simulated, average TO, as expected, increased across all species (Fig.4.4b). By the end of the global warming simulation, the average TO across species increased from approximately $12°C$ to $15°C$ (Fig.4.4). For the generalist/specialist (GS) trait, slow evolution towards the generalist strategy (lower GS indicates a wider thermal performance

window) occurred following the onset of simulated global warming (Fig.4.4d). Across species, mean GS changed from 9.5 to 8, equating to a widening of thermal performance windows by approximately $3°C$.

For the first 25 years of the global warming simulation these trait changes were mostly driven by the existing phenotypic diversity and changing relative abundances of phenotypes within each species, as seen by the relatively stable phenotype numbers during the early stages of warming (Fig.4.5b). This is because the trait value of a species is calculated as abundance weighted average across phenotypes. Hence a change in relative abundance of the phenotypes will affect the mean even if no new phenotypes are introduced or go extinct. However, after 50 years, phenotypic diversity was depleted (Fig.4.5b) and evolution was mostly driven by the appearance of new phenotypes and rapid changes in their relative abundance, driven by strong selective pressure.

4.4.2 Effect of mutation rates on phenotypic changes

The rate of evolutionary change during the global warming phase was critically dependent on the assumptions about the rate of new phenotype appearance (Fig.4.6). In the baseline scenario the probability of a new phenotype being generated at each time step was 0.003, leading to an average rate of change of 4.5% per year. Different rates of phenotype appearance had strongest effects from the year 50 onwards, i.e. starting around the time when existing phenotypic diversity was largely depleted (Fig.4.6c) and the rate of adaptation was largely driven by the rate at which new phenotypes appear. Three times faster phenotypic diversity generation rate naturally led to faster change of TO towards an increasing optimum, allowing the trait value to track environmental temperature more closely (Fig.4.6b; final TO values were $17°C$ for $\chi = 0.01$ versus $15.5°C$ for $\chi = 0.003$).

When rates of mutation were faster, the GS trait value did not decrease as fast as for the slow mutation rate, meaning species remained as specialists rather than shifting to a generalist strategy. In fact, for the fastest mutation rate ($\chi = 0.01$) the GS trait value for all species stabilised at around 8.75, while for the slowest evolutionary rate it continued to decrease over the course

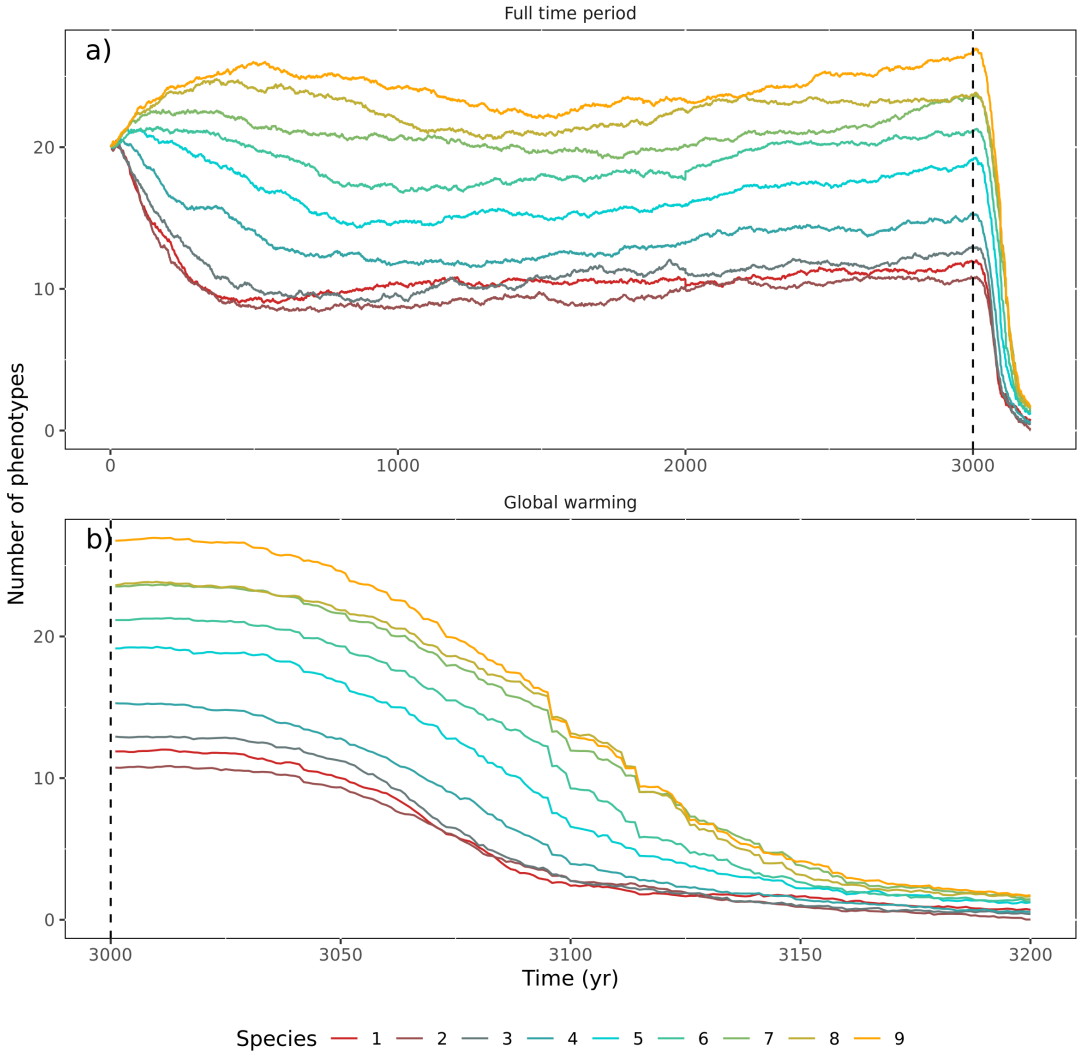


FIGURE 4.5: Mean number of phenotypes per species through time. The dashed colored lines show the standard deviation around the mean values. The dashed vertical line indicates the time were global warming conditions are enabled in the simulation. a) shows the entire period of the simulations, whereas b) zooms in on the global warming period.

of the simulation (GS = 8 at year 3200). This is because a slow mutation rate meant that TO trait could not track environmental temperature changes quickly or closely enough and the specialist strategy was especially disadvantageous. As expected, higher mutation rates led to a higher number of phenotypes maintained in the ecosystem after 200 years of global warming (30 versus 10 for χ = 0.01 and 0.003, respectively) (Fig.4.6c).

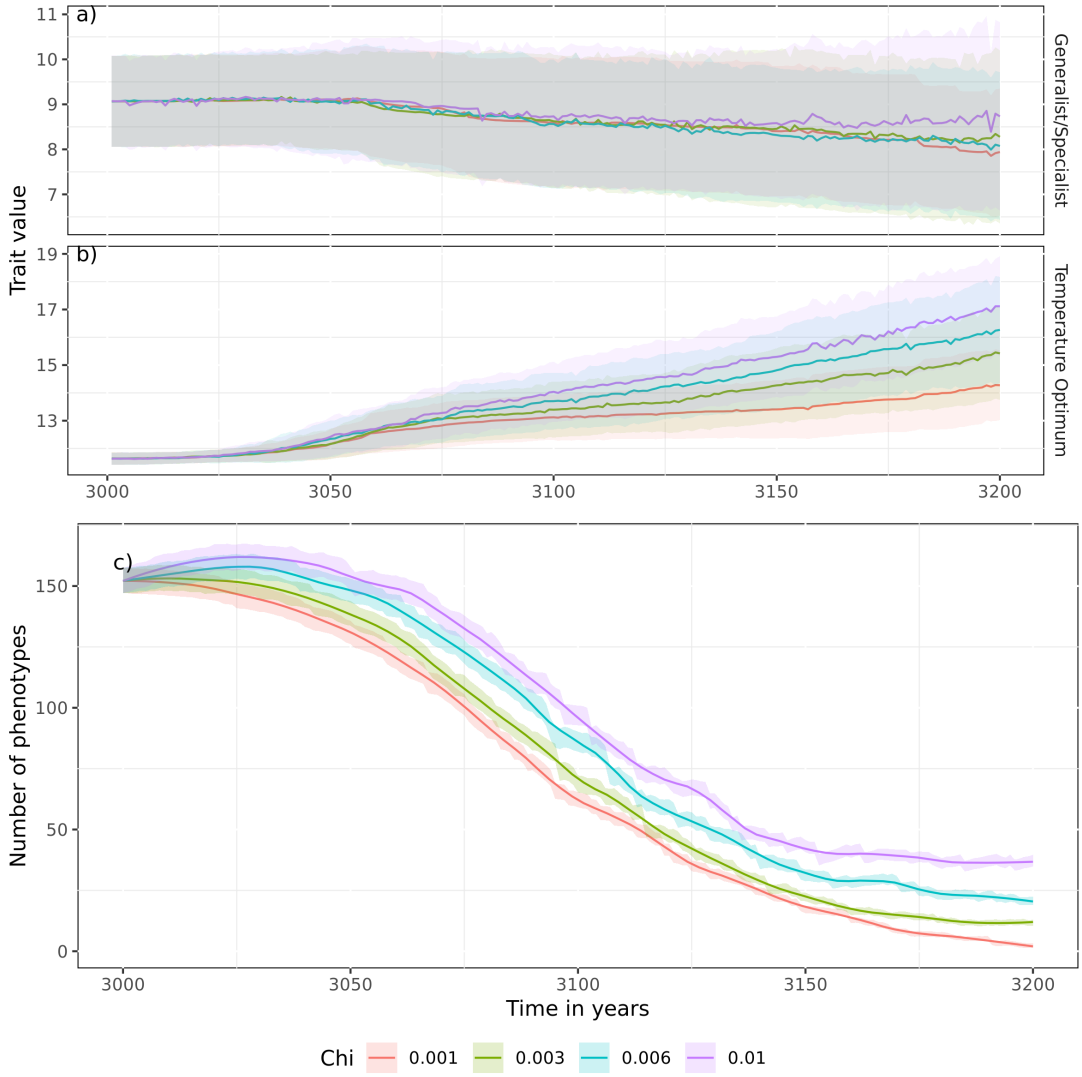


FIGURE 4.6: Effect of varying chi on the trait evolution averaged over species and simulations. a) shows the GS trait value (high is specialist while low is generalist). b) shows the TO trait value. c) is the number of phenotypes through time. The ribbons show the standard deviation around the mean. Only the variations during the global warming projections are shown. The chi value used in the main study is 0.003.

4.4.3 Impact of global warming on the fitness landscape

After 3000 years of adaptation to a stable climate, the fitness landscapes of TO and GS trait in all nine species had a similar wasp waist shape (Fig.4.7a), the only difference being overall higher fitness in larger species due to higher overall reproductive output. The highest fitness values were observed at TO values (x-axis Fig.4.7a) slightly above the yearly average temperature. Unexpectedly, being highly specialised or highly generalist had higher fitness values than intermediate values of GS (y-axis Fig.4.7a). Fitness per cohort is followed for 50 years

during the warming component of the simulations. For the first 50 years of warming (Fig.4.7b), the fitness of phenotypes with TO values slightly above the yearly mean temperature increased rapidly, whereas the fitness of phenotypes with TO values slightly lower than mean temperature remained more stable. The highest fitness values are observed at the edge of the fitness landscape at highest TO values (right side Fig.4.7b)

More patchiness in the fitness landscape started to appear after 50 years of global heating (Fig.4.7c), explained by a rapid loss of phenotypes (Fig.4.5b). As before the onset of warming, phenotypes with TO trait values slightly higher than the ambient temperature mean (vertical dashed lines in Fig.4.7) had higher fitness. Also, for most species (except 1,2 and 4) higher fitness values are seen at low GS values indicating that temperature generalists have higher fitness.

The final time slice (Fig.4.7d) showed a shift in the location and a reduction in the area of the fitness landscape, explained by the greatly diminished phenotypic diversity observed at the end of the simulations (Fig.4.5, 3100 to 3200 years), with only one or two phenotypes left per species. These extinctions contributed to the patchiness of the fitness landscape, as these landscapes were estimated from the results of all the simulations. A patchy landscape means that there were not enough data points from each simulation to interpolate a smooth landscape. In this case, the mutation rate was chosen to reflect reasonable estimates but it was not fast enough for trait changes to keep pace with the rate of warming. However, when the mutation rate was three times greater, the communities did not collapse for the largest species and they conserved the same pattern as previous time slices with increasing fitness gradient towards warm temperatures (Fig.S.5 in appendix D).

Note that species 3 was the only species to extend its phenotypic diversity to higher values of TO in relation to the mean ambient temperature, and for this species we observed the same fitness landscape as in Fig.4.7c, slightly inclined, with highest values of fitness in the bottom right corner (high TO and generalist) and the lowest values at the top left corner (specialist at low TO). For the other species, the yearly mean temperature was almost at the limit of their highest TO value (dashed line in Fig.4.7d at the limit of the fitness landscape window of most species).

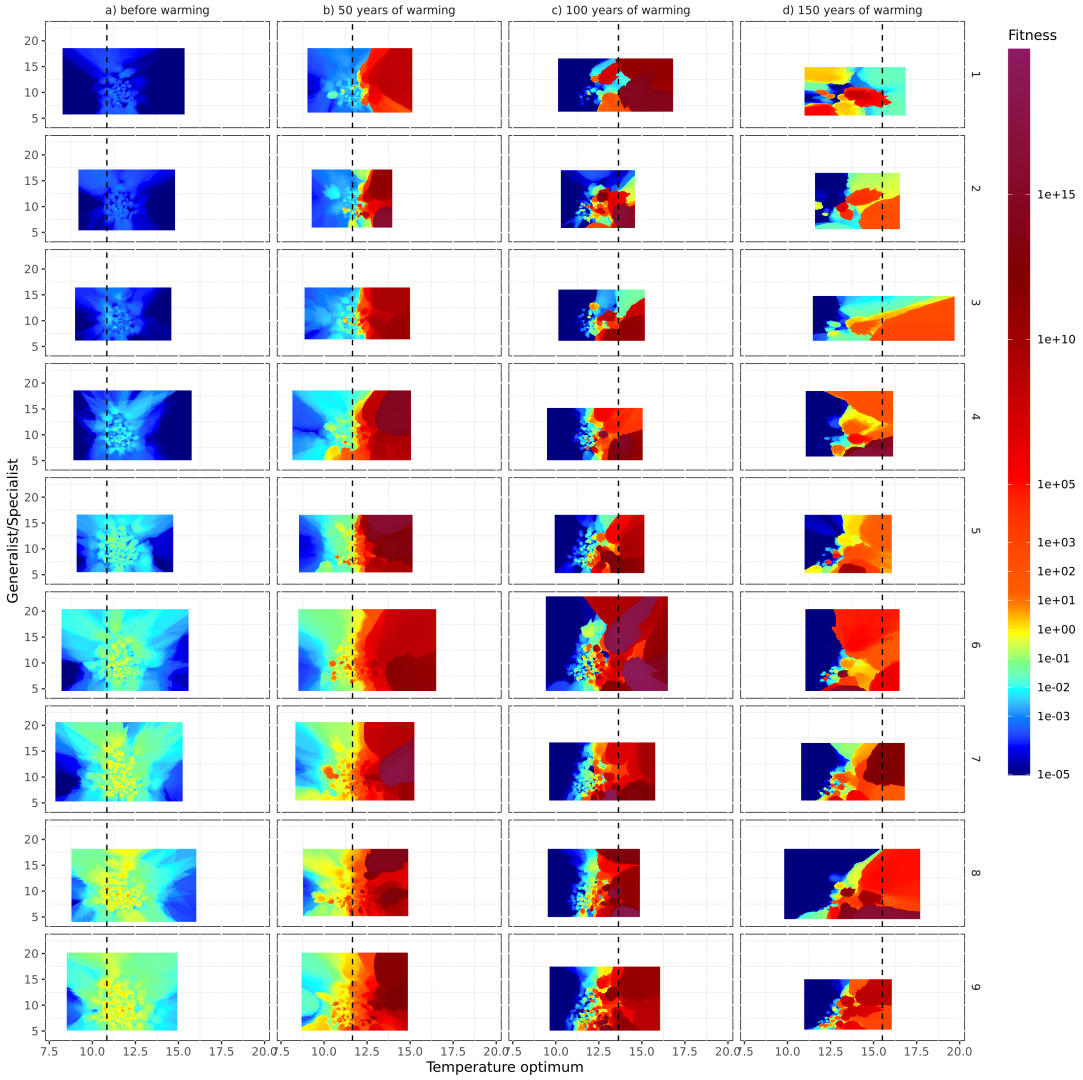


FIGURE 4.7: Fitness landscape per species during four different periods, before (a) and during global warming (b-d). The average individual spawn output throughout lifetime of a cohort of one phenotype within one species is used as fitness proxy. The landscapes are generated using the K-kernel nearest neighbour smoother on the fitness values of all phenotypes across simulations. The area covered by each fitness landscape reflects existing phenotype values taken at the time indicated in the panel title, such that larger areas represent a greater range of phenotypes. The species associated with each row of plots are listed down the right-hand side of the figure. The dashed lines in each column shows the mean temperature during that period of time (this value is different in each column and represents the warming trend in the simulations).

The average fitness values over the landscape peaked around 50-100 years of warming and then rapidly decline by 150 years of warming (Fig.4.7c, d vs Fig.4.7b). The phenotypic diversity had a limit and for this particular set of parameters, phenotypes did not appear fast enough to match the rate of extinction due to the warming. Hence after a hundred years, only a few phenotypes

per species remained and these phenotypes were still not well adapted to high temperatures, leading to a decrease in fitness.

Due to the large changes in phenotypic diversity within each species, we observed increasing variability in community biomass and slope of size spectrum over time (Fig.4.8). The mean community total biomass initially followed an increasing trajectory and then began to slowly decline around 150 years of warming simulation scenario. The variability across the environmentally stochastic simulations increased towards the end of the simulation period when heatwaves were more prevalent. The community size spectrum slope remained stable throughout most of the simulation, until the very end of the simulation when it declined and the variability across simulations increased markedly.

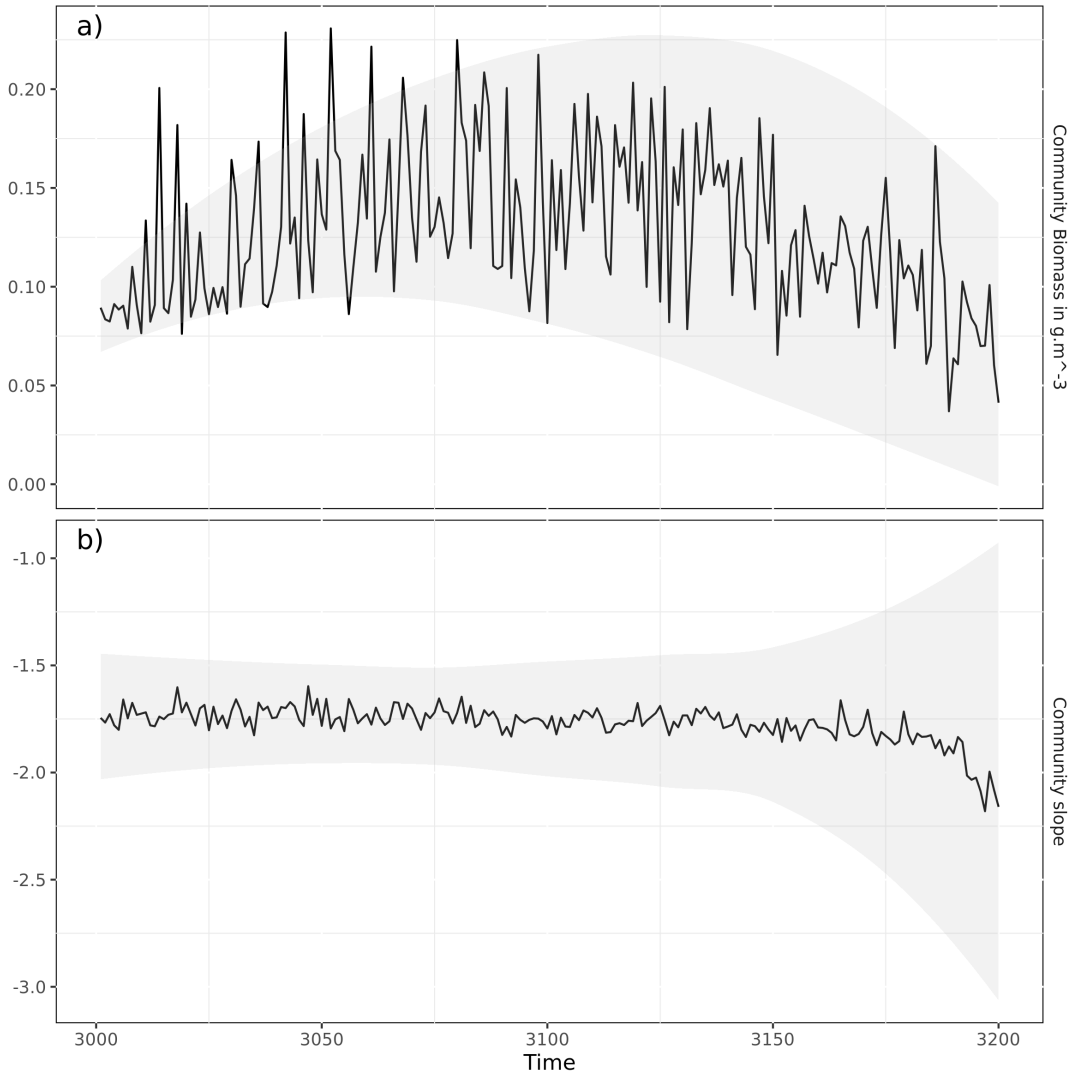


FIGURE 4.8: Change in community metrics in response to warming scenario. a) shows the mean total biomass across simulations at the community level during the global warming period. b) shows the mean slope of the size spectrum during the same period. The ribbon shows the standard deviation around the mean across simulations.

4.5 Discussion

The eco-evolutionary model presented here aimed to investigate evolutionary changes in fish thermal performance in response to global warming, and consequences for population and community dynamics. The model used simple rules of size-dependent predation, temperature scaling of physiological processes, and random introduction of new traits to assess adaptive changes of two temperature traits in response to rapid environmental warming and increasing heatwaves. There are three key findings of this study. First, we showed that, in the absence

of a climate trend, specialist thermal strategies prevailed in accordance with our expectations, with an average thermal performance window of $4°C$ (GS values of 10) and most species' thermal optima (TO) close to the long-term mean temperature conditions. Second, when global warming was introduced thermal optima changed more dramatically than generalist-specialist trait (GS), shifting on average by $4°C$ over 200 years of warming. However, the adaptive rate of TO was not fast enough to keep pace with the global warming projection towards the end of the simulation, and species gradually evolved towards thermal generalist strategies to help compensate. Third, the implications of these thermal adaptations for the modelled populations and communities included a gradual collapse in phenotypic diversity starting 50 years into the warming scenario. These changes in diversity were accompanied by gradual changes in total community biomass and size spectrum slopes that became more variable and declined as phenotypic diversity depleted.

4.5.1 Emergent strategies under a stable climate

The species predominantly converged and stabilized around one specific strategy: a TO slightly above than the annual mean temperature and being a thermal specialist, with narrower thermal windows for smaller species. It is important to note that these emergent strategies were partly influenced by two assumptions of our approach: (1) that "hotter is better", whereby we assumed that net food intake, and therefore reproductive output and overall fitness increase as optimal temperature (TO) increases. While the species in the simulation were free to evolve these traits given sufficient evolutionary rates, in reality there will be other limits and trade-offs at play. For example, it is clear that if hotter is to be better, organisms would need to have their entire physiology coevolved to hotter temperatures (Hochahcka and Somero, 2002; Somero, 2004). (2) The thermal performance curve was asymmetric, meaning that an ambient temperature above TO will have a large negative impact on thermal performance. Whereas an ambient temperature below TO will still cause a decline in performance but to a lesser degree. Therefore, it was beneficial for species to settle on a TO slightly above the annual mean temperature rather than exactly on it (consistent with Angilletta 2009). As a result, sudden changes in temperature, due

to seasonal and diurnal variability, did not decrease performance enough to cause the species to starve or go extinct.

Furthermore, as the temperature was relatively stable (no linear increase), but contained variability, several GS strategies emerged. Multiple GS coexisted with high fitness values, including more generalist or more specialist strategies. While generalists were able to have high fitness all year, specialists were able to compensate for the seasonal variation by having a higher fitness for a few months and low fitness for the rest of the year, yielding a fitness high enough to be competitive on average over the course of the year. Such an outcome was highly dependent on the strength of the generalist-specialist trade-off, which here was assumed to equate to a 50% higher scalar value at optimal temperatures, when the width of the thermal performance window was changed from 5 to $1°C$. Furthermore, the generalist-specialist trade-off can manifest within, as well as across, species, leading to more variation in phenotypic diversity than with the "hotter is better" trade-off (Phillips et al., 2014), which may explain the greater variation observed in this trait.

4.5.2 Adaptations to global warming

Field data on thermal performance are often based on the frequency of occurrence at different environmental temperatures (such as Waldock et al. 2019). Often species' optimal temperatures are assumed to be static, which our model shows to not be the case. Here, all species adapted to warming by undertaking shifts in both thermal performance traits in response to both an increase in temperature and an increase in temperature anomalies. Specifically, we saw an increase in TO and a widening of thermal performance windows, the latter measured as decreasing GS (move to generalist strategy). These adaptations prevented immediate community collapse. Thus, evolutionary rescue occurs when natural selection acts fast enough to prevent population collapse and extinction. Using eco-evolutionary consumer-resource network models, Yacine et al. (2019) showed that switching off or slowing down of evolutionary rates led to higher biodiversity loss under warming. This indicates that eco-evolutionary feedbacks may help protect species diversity against global warming.

Evolutionary rescue also depends on the population's baseline extinction risk (Peniston et al., 2020), which in our simulations depended on the initial phenotypic diversity before warming (more phenotypes coexisting means lower risk of extinction). We observed a gradual loss of phenotypic diversity, which in turn led to the collapse of some species and a shift in community size structure towards the end of the simulation period. This is in line with other studies showing that evolutionary rate is unlikely to keep up with the pace of global warming (Gienapp et al., 2008; Ozgul et al., 2010; Hoffmann and Sgrò, 2011). In our model, faster evolutionary rates (three times faster) led to species adaptations that managed to keep up with the rate of temperature increase. However, the main challenge is knowing the correct evolutionary rate, and indeed previous work has called for greater cooperation between geneticists and evolutionary biologists (Kokko et al., 2017). Better understanding of the speed at which species temperature optima and width can change could help improve models and therefore provide insight on the scope for future thermal adaptation for marine ectotherm against warming temperatures.

4.5.3 Model limitations and future needs

We assumed that size had no impact on the shape of the performance curve in our model or the evolutionary rates in our model. This may explain why we found no size-specific trend in terms of thermal performance adaptation: small species and large species developed the same adaptations to temperature. However, size affects intraspecific variability in temperature performance but the direction of the relationship between size and the shape of the performance curve is lacking (Lindmark et al., 2018b). Furthermore, body size may affect the speed at which organisms are able to adapt (Gillooly et al., 2005). Empirical studies show that small organisms with short generation spans, such as rotifer-alga (Yoshida et al., 2003) and phytoplankton-zooplankton (Hulot et al., 2000) may evolve at a rate that follows temperature increase due to global warming.

We used a constant evolutionary rate through time and did not consider any influence from temperature on this process. However, Gillooly et al. (2005) shows that body size and temperature control organisms' rates of evolution through their effects on metabolism, creating dynamic

evolutionary rates through time. Towards the end of our simulations, the fish communities collapsed due to a loss of phenotypic diversity that was not replenished fast enough to ensure ongoing integrity of the community. This suggests that in locations where phenotypic diversity of thermal performance is narrow, such as areas with historically stable temperature regimes e.g. the tropics (Walters et al., 2012), there will be a lower probability of species adapting to warming temperatures.

While we recognize that continuous reproduction does not allow for a biological match to the seasonal forcing of temperature, we are working within a trait-based framework which does not provide a general trait-based equivalent for species' seasonal reproduction, in terms of energy allocation towards maturation and spawning. To enable this would need to use a multi-species framework with realistic species-specific parameters introducing seasonal variability in the spawn output (as in Datta et al. 2016). Also, we have assumed stringent rules regarding density dependence to constrain reproduction and promote coexistence as in other trait-based model papers (Andersen and Pedersen, 2010; Jacobsen et al., 2013). No variations emerged in the realised recruitment of the smaller size classes, which can be explained by our density dependence assumption. As a future broader study this would be a very interesting trait to look into for future applications of mizerEvolution, to determine which types of spawning patterns emerge under which environmental conditions. However, it is outside the scope of the current study.

The evolutionary component of our model did not consider acclimation which influences the thermal performance of organisms in real ecosystems and can act as a buffer to fast temperature changes (Bozinovic et al., 2013). However, experiments support the adaptation of TO to increased temperatures (mesophile in Kosaka et al. 2019; phytoplankton in Padfield et al. 2016; fish in Huss et al. 2019). Support for the temperature generalist strategies is scarce (Angilletta, 2009). Although multiple studies have highlighted the importance of thermal variability, and its effect on overall thermal performance (Folguera et al., 2009; Vázquez et al., 2017; Bozinovic et al., 2013; Paaijmans et al., 2013), whether these findings hold empirically needs to be tested.

We chose to represent global warming with a stylised rcp8.5 scenario. We used the rcp 8.5

scenario as other rcp scenarios are reliant on the assumption that we will lower our carbon emissions, a goal we have yet to attain (http://www.globalcarbonatlas.org/). Moreover, this was an initial exploratory study and as such it was best done testing it under strong change; once those conditions are understood then we can move into more complex variation patterns (e.g. under the lowest rcp cases) and where factors other than temperature may have large confounding roles. Lotze et al. (2019) explores two climate models with four emission scenarios that were used to force an ensemble of six global marine ecosystem models, which did not include any eco-evolutionary processes. Their study found that biomasses declined across all scenario, albeit to different extents. Whether or not the inclusion of eco-evolutionary processes in global and regional ecosystem models would buffer these changes could be addressed by comparing models with and without evolutionary processes, with empirical data.

4.5.4 Conclusions

The consequences of climate change for ecosystem structure and biodiversity will depend on phenotypic diversity, the rate of warming versus rate of adaptation, and the structure of ecological communities. Our study has contributed to this by showing that eco-evolutionary dynamics allowed species to adapt to global warming but adaptation was not going to be fast enough to sustain increasing temperatures in the long-term. However, better estimates of adaptation rate of traits of marine taxa are now needed to help advance models and the understanding they provide. Furthermore, ecosystems are not only affected by warming, but also by other anthropogenic changes, such as nutrient availability or habitat fragmentation, which are also known to affect food web structure (Calcagno et al., 2011; Pillai et al., 2011; Post, 2002). Integrating the impacts of these different anthropogenic drivers into size-based models will be essential to improve understanding over future shifts in ecosystem structure and function.

4.6 Tables

TABLE 4.1: Model equations for each species' ecological dynamics. Subscripts for each species are not included in the equations below for readability. These dynamics also hold for each phenotype (nested within each species) once they have entered the size spectrum. Equation numbers reference the processes illustrated in Figure 2.1 and descriptions in main text. $N(m)$ is the density at size driven by: $g(m)$ which is the feeding dependent growth rate at size and $\mu(m)$ which is the mortality at size, the latter is comprised of several mortality terms below. All parameter values and definitions are provided in Table 4.2 or the main text.

Equation	Description	
Species population dynamics	$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$	(E1)
Background resource dynamics	$\frac{\partial N_R(m,t)}{\partial t} = r_0 m^{p-1}\left[\kappa_R m^{-\lambda} - N_R(m,t)\right] - \mu_p(m)N_R(m,t)$	(E2)
Temperature scaling	$r(T,T_{ref}) = e^{\frac{E_A}{k}(\frac{1}{T}-\frac{1}{T_{ref}})}.(1+e^{\frac{E_D}{k}(\frac{1}{T}-\frac{1}{T_D})})^{-1}.(1+e^{\frac{E_D}{k}(\frac{1}{T_{ref}}-\frac{1}{T_D})})$	(E3)
Prey size selection by size m predator	$\phi(m,m_p) = exp\left[\frac{-(ln(m/(\beta m_p)))^2}{2\sigma^2}\right]$	(E4)
Encountered food by size m predator across all sizes (mp) of species j prey	$E(m) = \gamma m^q \int \left(N_R(m_p) + \sum_j \theta_j N(m_p)\right)\phi(m,m_p)m_p \mathrm{d}m_p$	(E5)
Feeding level	$f(m) = \frac{E(m)}{E(m)+hm^n}$	(E6)
Energy allocation towards reproduction	$\psi(m) = \left[1+\left(\frac{m}{m^*}\right)^{-u}\right]^{-1}\left(\frac{m}{M}\right)^{1-n}$	(E7)
Somatic growth	$g(m) = (\alpha f(m) h m^n - k_s m^p)(1-\psi(m))$	(E8)

Reproduction	$$R_p = \frac{\epsilon}{2m_0} \int N(m)(\alpha f(m) h m^n - k_s m^p)\psi(m)\mathrm{d}m$$	(E9)
Recruitment	$$R = R_{max} \frac{R_p}{R_p + R_{max}}$$	(E10)
Predation mortality on size mp prey inflicted by all sizes (m) of species j predators	$$\mu_p(m_p) = \sum_j \int \phi(m, m_p)(1 - f_j(m))\gamma_j m^q \theta_j N_j(m)\mathrm{d}m$$	(E11)
Senescence mortality	$$\mu_{se} = \begin{cases} se_{min} + (se_{max} - se_{min}) e^{-\frac{M}{m}}, & \text{if } m > m^* \\ 0, & \text{otherwise} \end{cases}$$	(E12)
Starvation mortality	$$\mu_{st} = \begin{cases} st_r m\left(k_s m^p - \alpha f(m) h m^n\right), & \text{if } k_s m^p > \alpha f(m) h m^n \\ 0, & \text{otherwise} \end{cases}$$	(E13)
Background mortality	$$\mu_b = \mu_0 M^{n-1}$$	(E14)
Fishing mortality	$$\mu_f = \begin{cases} 0.8, & \text{if } m >= m^* \\ 0, & \text{otherwise} \end{cases}$$	(E15)

TABLE 4.2: Parameters table. M is noted "variable" as it is species specific (values in Table 4.3). T_D and E_D are noted "variable as they will change during the simulations, similarly T_{ref} and E_A are respectively linked to the previous two parameters and will vary in consequences. Parameters values are taken from Hartvig et al. (2011). The value from γ was calculated from: $\gamma = h\frac{f_0}{\sqrt{(2\pi)}\sigma\beta^{\lambda-2}e^{((\lambda-2)^2\sigma^2/2)}\kappa(1-f_0)}$ (Hartvig et al., 2011). Initial values for the abundance density $N(m)$ of each species at $t = 0$ were based on the equilibrium equation: $N = \frac{\kappa}{1000}M^{(2n-q-2+0.35)}m^{(-n-0.35)}$ provided in Andersen and Beyer (2006).

Symbol	Value	Units	Parameter
Individual growth			
M	variable	g	Asymptotic size
η	0.25	-	ratio between M and m^*
m^*	ηM	g	Maturation size
f_0	0.5	-	Initial feeding level
γ	538	$g^{-q}m^3yr^{-1}$	Factor for search volume
α	0.6	-	Assimilation efficiency
h	85	$g^{1-n}year^{-1}$	Maximum food intake
n	0.75	-	Exponent for max. food intake
p	0.75	-	Exponent for standard metabolism
ks	4	-	Factor for standard metabolism
β	100	-	Preferred predator-prey mass ratio
σ	1	-	Width of the feeding kernel
q	0.8	-	Exponent of search volume
Reproduction			
m_0	0.1	mg	Offspring mass
ϵ	1	-	Efficiency of offspring production
u	7	-	Width of maturation transition
Mortality			
ξ	0.1	-	Fraction of energy reserves
μ_0	2	$g^{1-n}year^{-1}$	Background mortality
se_{max}	1	$g^{1-n}year^{-1}$	Upper limit for senescence mortality
se_{min}	0.1	$g^{1-n}year^{-1}$	Lower limit for senescence mortality
st_r	0.1	$year^{-1}$	Starvation mortality cost
θ	variable	-	Interaction matrix species-specific value
Resource spectrum			
κ	0.05	$g^{\lambda-1}m^{-3}$	Magnitude of resource spectrum
λ	$2-n+q$	-	Slope of resource spectrum
r_0	4	$g^{1-p}year^{-1}$	Regeneration rate of resources
m_{cut}	1	g	Upper limit of resources spectrum
Evolution			
χ	0.003	-	Phenotype's introduction probability
Ω	10^{-30}	$individual/m^3$	Extinction threshold
	5%	-	Fraction of initial phenotype's abundance
ζ	$+-20\%$	-	Magnitude of trait evolution
Temperature			
T_{ref}	variable	$°C$	Temperature reference
T_D	variable	$°C$	Deactivation temperature
E_A	variable		Activation energy
E_D	variable	-	Deactivation energy

TABLE 4.3: Initial maturation, asymptotic size and R_{max} of the species.

Species	Maturation size (g)	Asymptotic size (g)	R_{max}
1	2.5	10	0.49208
2	8	32	0.19854
3	25	100	0.08011
4	79	316	0.03232
5	250	1000	0.01304
6	790	3162	0.00526
7	2500	10000	0.00212
8	7905	31622	0.00085
9	25000	100000	0.00034

Chapter 5

General discussion

Understanding how biodiversity variation and loss affects ecosystem function is one of the grand scientific challenges for ecology and is needed to help address global biodiversity policy goals (e.g. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services). Social-ecological systems are complex systems comprised of many different organisms and the interactions among these organisms, the environment and people give rise to variability and changes in biodiversity patterns we observe (including within species, between species and of ecosystems e.g. the United Nations Convention on Biological Diversity Aichi Biodiversity Targets). Given the complexity of these systems, ecosystem and community models are tools we can use to improve this understanding. In this era of environmental change, most marine ecosystem models struggle to provide output that captures the true adaptive capacity and level of change observed in current ecosystems and expected of future ecosystems. This compromises the capacity of researchers and decision makers alike, as we need information on how systems are likely to respond to better support planning and decision making and meet policy goals.

Until recently, dynamic marine multispecies, community and ecosystem models commonly stand with one of these assumptions:

1. Species composition is fixed
2. Trait-based models that do allow for species composition flexibility assume that traits themselves are fixed

3. Evolutionary models which allow for trait changes through time usually assume that evolution is slow and that systems should be in eco-evolutionary equilibrium conditions. This means that traits are still fixed over ecological or politically relevant time scales

In the introduction of this thesis, I suggested that the complex adaptive system (CAS, Holland 1992; Levin 2003) framework could help move dynamic marine multispecies models beyond these assumptions. CAS provide a starting point to consider how one could capture continuous changes in traits and species in marine community and ecosystem models. I have summarised that the key characteristics of CAS are (Levin, 1998): 1. Diversity and individuality of components (e.g. individuals); 2. Localized interactions among those components; and 3. An autonomous process that uses the outcomes of those interactions to select a subset of those components for replication or enhancement (e.g. adaptation). While, CAS do not have any explicit requirement for equal timescales, the field of eco-evolutionary modelling has provided both the rationale and capability for ecology and evolutionary processes to be modelled over the same timescales (Matthews et al., 2011). Therefore, a CAS framework with eco-evolutionary dynamics can provide a way to overcome the aforementioned three restrictive assumptions of used in marine community and ecosystem models.

This thesis combines the advantages of an eco-evolutionary approach with existing size and trait structured modelling methodologies, contributing to advancing marine ecosystem models in the context of CAS in the following ways:

- Enabling phenotypic eco-evolution within species in complex size-structured dynamical communities
- Providing new insights into the long-debated question on the interplay between natural (i.e. predation) and fisheries induced selection in driving evolution of maturation size
- Assessing how size structured communities might self-organise in terms of feeding traits (predator prey mass ratios, PPMR) along the productivity gradient
- Comparing trade-offs among different types of thermal adaptations under climate change and the ability of ecosystem to adapt to rapid environmental change

The thesis shows that by allowing random introduction of new phenotypes on ecological time scales and assuming trade-offs between key traits, even simple physiologically structured multi-species models can produce results compatible with empirical observations of fish communities.

5.1 MizerEvolution as a Complex Adaptive System

The core methodological output of my thesis is the evolutionary model MizerEvolution. To explore eco-evolutionary dynamics in multi-species systems I needed a modelling tool that represents a complex adaptive system (CAS) but allows for evolution in ecological time scales. Thus, it is important to evaluate how MizerEvolution aligns with the key components of a CAS. CASs require individuality of components. While formulated around the individuals-level processes, trait-based size spectrum models are not individual-based models and phenotypes used in MizerEvolution cannot really be considered as individuals. Furthermore, the diversity of the phenotypes is limited by the number of studied traits, with many parameters remaining fixed in the model. Nevertheless, in my model, phenotypes are independent of each other, are the smallest unit of a multi-layered ecosystem (phenotypes, within species within a community), and are diverse enough that changes in their identity translates into trait changes at the ecosystem-level. Combined with their random introduction, phenotypes do enable the model to exhibit self-organising behaviour from lower to higher levels of organisation.

The second characteristic of CAS is localised interactions. Once we accept that phenotypes are the smallest component in the model, phenotypes are free to interact via predation or resource competition with any other phenotype present within the system. Their interactions are not individual-based and their action usually will target size classes across phenotypes, yet interactions are not done over entire species at a time, so they approximate local interactions.

The third requirement is an autonomous selection process which enhances the components. This process comes from three different factors of the model. The first is the random introduction of new phenotypes, adding new components to the model continuously; second, I add the fact that phenotypes can go extinct if they do not fare well in the ecosystem; and third, time. The

combination of these three factors recreate natural selection in the model constantly removing unfit phenotypes and allowing fit ones to reproduce, based on how they interact with their environment. In conclusion, this model can be considered a CAS of marine food web and one that provides useful insight into potential evolutionary adaptation responses.

5.2 Development of MizerEvolution

MizerEvolution is now available as an R package extension to the Mizer R package (Scott et al., 2014). Publication of a package extension ensures the model framework will be available and accessible for future applications to develop further understanding of eco-evolutionary processes.

The documentation of MizerEvolution, showing how to set up a model and detailing the key diagnostics involved is provided on https://github.com/baldrech/mizerEvolution. Briefly, the model mimics evolution by simulating the phenotypic plasticity within species. This pool of phenotypic diversity is constantly replenished with random trait values (related to the existing trait values within the species) and from this randomness emerges evolutionary patterns, if the selection within the model is strong enough to push the less fit phenotypes to extinction. This framework allows users to choose any explicitly modelled traits and any evolutionary rate to be able to model evolutionary dynamics in a size-structured context. I only explored the effect of the adaptation of a few traits (maturation/asymptotic size ratio, PPMR, temperature optimum and temperature generalist/specialist) and only in one case with two traits evolving at a time (thermal strategies). However, in developing a freely available extension to the Mizer package, this thesis will directly contribute to the capacity necessary to explore a wider range of traits and multiple evolving traits. While the modelling tool does not allow for individual level processes, it provides an important benefit of being able to model dynamic (i.e. not evolutionary stable states) ecosystem evolution with minimal computing power. This approach contrasts with popular evolutionary models that are computationally expensive; run for millions of (model) years; and do not consider eco-evolutionary dynamics. The three chapters of this thesis apply the modelling tool to address three long-debated questions in evolutionary ecology.

5.3 Overview of key findings

5.3.1 Maturation size declines due to fishing – for some but not all species

In Chapter 2, I explore the interplay of natural and fisheries induced selection on maturation size in a multi-species system. My model adds evolution to a size-structured model using a simple approximation that begins at the level of phenotypic diversity within a species and does not capture the details of genetics, heredity and mutations (as in quantitative genetics model, Lynch and Walsh 1998; Lande 2007; Lively 2012; Engen et al. 2013).

This approach is conceptually similar to adaptive dynamics, with the important exception that ecological and evolutionary timescales are not separated. The model is technically similar to other eco-evolutionary food webs models where random distribution of traits are introduced at every timestep (Ito and Ikegami, 2006; Takahashi et al., 2013; Allhoff et al., 2015; DeLong and Gibert, 2016), but differs by having the same time scale of evolutionary and ecological processes. Finally, while my work is the first to consider such an eco-evolutionary approach within a marine size-structured model, the approach is an accepted method, with the use of eco-evolutionary dynamics within size-structure already employed in plant models (Falster et al., 2016).

In this chapter I show that by introducing trait evolution on system dynamics and assuming simple trade-offs between maturation, growth and mortality leads to a range of changes and emergent patterns across different sized species through time. With no external constraints on maturation size in the model, the emergent patterns corresponded to general empirical patterns – i.e. small fish always mature fast and die fast (Charnov et al., 2013) whereas maturation size of large species depends on the strength of fisheries selection (Heino et al., 2015). Importantly, this work shows that responses of medium-sized species are highly variable. This variability appears to be driven by a tug-of-war between the impacts of predation and fisheries selectivity. Fisheries mortality selects for a decrease in maturation size, but predation mortality on juveniles pushes species toward fast growth and delayed maturation. This chapter highlights how intra- and inter-species interactions have a considerable impact on maturation size in fish communities.

This work emphasises a need for predation interactions and rapid evolution to be taken into

account in studies of fishing-induced evolution to support understanding of the effects of different management actions. For example, recent work has suggested than balanced harvesting that keeps fishing mortality in line with natural productivity across the size spectrum, could be a sustainable option by maintaining maturation size over time (Law and Plank, 2018). This thesis suggests that these findings now need to be evaluated when allowing for predator-prey interactions and rapid evolution, the impact on medium-sized fish is uncertain as they would not benefit from the predation release from large fish which would be added to the fisheries mortality.

Another key aspect of this study demonstrates that inter-specific competition for resources and predator-prey interactions can have important effects on the evolution trajectories of the species as without fisheries pressure, predation mortality determines the adaptation towards the most efficient maturation size (i.e., small species mature fast and die fast versus larger species growing fast and maturing later in life). Since competition between species can make them evolutionary diverge (Schluter, 2000), or converge (terHorst et al., 2010), more detailed work on competition and how it interacts with evolution is necessary to construct better food web models. Recent advances in eco-evolutionary size-structured models for plant communities have shown that reproduction and growth patterns are influenced by competition, and how modelling competition for a resource allows for the emergence of different growth strategies (Falster et al., 2016).

Of course, each study has limitations and leads to many new questions. One limitation of the approach taken here is that we do not model genetic basis of evolution but approximate it by introducing phenotypes randomly from a normal phenotypic distribution. My assumption is that in the long term, a model using genetics as a base for mechanistically reproducing phenotypic diversity would give approximately the same qualitative trends as our simplistic version. Furthermore, the more we consider evolutionary processes, the more problems get exponentially complex. For example, just deciding that only one trait governs the maturation size instead of considering all the cascading genes controlling the growth and reproduction of individuals, how they are inherited and how often they are subject to mutations, will of

course decrease accuracy in my results, but considerably quicken the modelled process of evolution. Another limitation is that fisheries and species composition scenarios applied here were necessarily simplified, assuming same fishing mortality for all species in the ecosystem and that species maximum sizes in the ecosystem are equally spaced. Future studies could apply the framework developed here to a more realistic ecosystem and assess the likelihood of different fisheries selectivity patterns translating into desired management outcomes. If the objective is to have sustainable fisheries which minimise the evolutionary impacts, we need to consider how targeting of single species affects the food web more broadly. If one large species is affected (such as shown in Chapter 2) it is likely to have impacts on the rest of the food web. From this starting point a larger set of questions can be asked about the more complicated multi-species fisheries.

5.3.2 Emergent strategies for predator – prey mass ratios depend on resource level

Predator-prey mass ratios (PPMR) of species have been widely studied and are useful as proxies to explain non-random food web structure and body size constraints on who eats whom (Cohen et al., 2003; Williams and Martinez, 2000; Beckerman et al., 2006). PPMR has been reported to influence ecosystem function, structure as well as stability (Brose, 2010; Brose et al., 2019; Blanchard et al., 2008) and PPMR will vary across different resource levels – e.g. low resource levels lead to higher competition and divergence of feeding traits (Gravel et al., 2019).

In Chapter 3, we examined how adaptive changes in species' predator-prey mass ratios might depend on the level of resource availability. Starting with an equal PPMR for all species, we explored the influence of resource level on the evolution of PPMR across and within species. The model revealed that under low resource levels, most species evolve towards higher PPMR values, and this is especially strong for the largest species. The inverse was true with high resource levels, allowing for the emergence of predators with low PPMR values (piscivory). The emergent PPMRs in the study were consistent with broad empirical patterns (Barnes et al., 2010), where large species generally had higher PPMR ($\sim$ 10000 PPMR and $\sim$ 10kg; similar to

e.g. *Atlantic Cod*) and smaller species had lower PPMR (~ 100 PPMR and ~ 10g; similar to e.g. *John Dory*), and where large planktivore species evolve specific adaptations (e.g. baleen whales) access highly abundant small planktonic prey to support their own large sizes and energy requirements. I should note that baleen whales have different life histories and metabolic requirements than the "teleost"- centric size spectrum model used here and therefore they may not adequately capture their dynamics with my current model assumptions. Nevertheless, the 'high PPMR' marine animals feed on much smaller prey than themselves and by-pass the typical size-based food chain, where (on average) many fish are assumed to feed approximately 100-1000 times smaller than themselves (Jennings and Warr, 2003). The study therefore shows that emergent PPMR in the system is influenced by more factors than predation traits alone, which could potentially explain the huge range of PPMR found in marine ecosystems (Brose et al., 2019).

The study shows that under high resource levels the PPMR strategies bifurcate, allowing for the emergence of both planktivorous (high PPMR) and piscivorous (low PPMR) strategies. Such bifurcation might help explain why food web structure differs between ecosystems with different resource availability. It also illustrated how the evolution of PPMR can allow for increased top-down control on the structure of the food web. Moreover, it highlights that exploiting these large species, or even their prey, could potentially affect eco-evolutionary adaptations leading to a change in PPMR value, with the resulting consequences on energy transfer efficiency, food web structure and destabilising exploited food-webs (Andersen, 2019). Yet, despite these consequences for food web structure, the study showed that under different resource levels, the species adapted in such a way as to conserve the size spectrum slope, which has also previously been found in other size-spectrum models (Heneghan et al., 2016). This suggests, at least in the absence of exploitation, that adaptation acts to stabilise the size structure of the community.

One limitation of my modelling approach was that I used only an ontogenetically constant mean PPMR with respect to predator size (i.e. the PPMR value stays the same during the organism's lifetime), with variation captured by a lognormal distribution of individual level PPMR. In reality, a wider range of predator: prey size relationships exist for both aquatic and terrestrial

environments, from mosquitoes to large mammals (Elton, 1927; Carbone et al., 1999; Nakazawa et al., 2013; Tucker and Rogers, 2014), where juveniles and adult of the same species do not have the same PPMR (e.g. PPMR decreases or increase with size throughout ontogeny). I have already noted that I may not have faithfully captured the dynamics of large marine mammals, even if the model produced similar PPMR patterns to those seen in baleen whales. The model, which is heavily teleost focused, also fails to capture the diversity of dynamics seen in invertebrate species. For example, a large diversity of feeding modes exists in small zooplankton, which can have low as well as extremely high PPMRs, but are also non-constant in relation to predator size (Hansen et al., 1994; Wirtz, 2012). This will be a useful topic for future exploration. Moreover, the flexibility of this modelling framework, which allows for different feeding kernel functions to be represented, provides an excellent launch point for future work that could widen the scope for understanding PPMR adaptation in a broader sense (Blanchard et al., 2017a).

5.3.3 Adaptive thermal strategies buffer short but not long-term warming scenarios

In chapter 4, I used the MizerEvolution model to explore community adaptation to climate change scenarios. In this case two traits, related to species' thermal performance strategies, were allowed to evolve. For simplicity I assumed that the traits are inherited independently, and their co-evolution is driven only through the emergent phenotype performance.

As this was a proof of concept approach, I considered a stylised climate experiment: a long-term stable climate scenario versus a long-term worst case climate scenario (i.e. as predicted under high emissions scenarios). The stylised scenarios were constructed based on the key features of temperature change (mean trend, standard deviation through time) from the IPSL Earth system model, extracted and spatially averaged for a climate change hotspot - the South-eastern Australian large marine ecosystem. As such, we did not attempt to capture the breadth range of uncertainty across climate change projections captured by an ensemble approach. Rather we took a "what if" approach to the study, with the aim of exploring the extent to which adaptation in thermal preference could occur under extreme scenarios, relative to a longer term but realistic

baseline. This provides a theoretical basis for understanding the process based bias present in current large scale climate ocean ecosystem projection work (e.g. FISH-MIP; Blanchard et al. 2017b; Lotze et al. 2019), the bias that does not account for eco-evolutionary changes that will inevitably shape the systems. The results of this chapter highlighted that under baseline assumptions about the rate of evolution, generic modelled species can handle the increase in temperature at the cost of their phenotypic diversity, but only for a short period of time (50 years in these simulations). However, the evolutionary rate used in this chapter is a conservative assumption and better knowledge of the species temperature optima and width evolutionary rate could help improve the model which called for greater cooperation between geneticists and evolutionary biologists (Kokko et al., 2017). This indicates that future projection work needs to take into eco-evolutionary mechanisms if it is to better inform discussions of the implications of climate change for fisheries and food security.

In this chapter, biodiversity change was assessed through phenotypic diversity and richness and the consequence for ecosystem function as measured by characteristics of the community through fitness landscapes. However, these metrics are not enough to fully quantify the consequences of our model scenarios on biodiversity and ecosystem function. Using a trait-based size spectrum model, Maureaud et al. (2020) recently showed that species dominance, species composition, trophic structure and environmental trait space influenced the biodiversity and function of ecosystems. They showed that two ecosystems with same species richness will have a very different network structure depending on the species dominance for example. Similarly, using the allometric trophic network model, Allhoff and Drossel (2016) showed that functional diversity (measured as the area of all feeding kernels within the ecosystem) could vary significantly and would not be noticed in their measure of ecosystem functioning (metabolic loss, consumption rate, total biomass). Analysing these metrics from our model outputs would help us to better understand the potential consequences of changing thermal strategies on food web structure, function and biodiversity.

The key uncertainty of the study relates to the speed at which evolutionary rates occurs. How fast evolutionary rates should be parameterised in models is not well understood, and moreover,

levels of existing genetic variance that allows for rapid adaptation will also vary across the species. Evolutionary rescue, where evolution enables species to survive severe environmental change, has been shown to help against global warming (Yacine et al., 2019) by reducing the long-term diversity loss due to increasing temperature. In the model the fastest evolutionary rate only helped species to keep up with the rate of warming, albeit with some loss in phenotypic diversity. However, among the different evolutionary rates tested, the fastest one seems unrealistic as it is 10 times higher than what we use to measure the fisheries induced evolution of maturation size in chapter 2 and was only simulated to see how fast evolution needs to be to compensate global warming. Yet, life-history evolutionary rates may not necessarily reflect potential evolutionary rates in traits related to thermal performance. Gillooly et al. (2005) shows that smaller organism and warmer environment both lead to faster evolution rate, therefore an important next step is the use of experimental systems to explore evolution in species with short generation times to be able to calibrate our model's evolutionary rate. As a final precaution it should be noted that appearance of new phenotypes in my studies approximates both the phenotypic evolution driven by existing genetic variance (i.e. quantitative genetic framework), and due to any new mutation that might arise. The interplay of these factors and the best way to incorporate them into a computationally efficient framework remains one of the key challenges in eco-evolutionary multi-species models.

5.4 Where this model fits within other approaches

Models focusing on eco-evolutionary dynamics take two main approaches with respect to how they incorporate evolution (Govaert et al., 2019): 1) rapid evolutionary models using quantitative genetics (Lande, 2007; Lively, 2012; Engen et al., 2013) or 2) slow evolutionary models using adaptive dynamics (Zhang et al., 2015; Meng and Zhang, 2016; Doebeli and Ispolatov, 2017). My model aligns more closely to rapid evolutionary models but does not use quantitative genetics to model evolution, which usually determines a trait value issued from genetic variations at the population level. The difference here brings us closer to an individual-based model (IBM) approach, since we model the phenotypic diversity within a species instead of having an

approximation of the average trait value (quantitative genetics). We do not track every individual through time, as in an IBM, but rather the abundance - size distributions (or demography) of phenotypes as dictated by their rates of growth and death and reproduction. Therefore, our model makes simpler assumption than a quantitative genetic model, but tracks more diversity in a mechanistic way due to the phenotypic diversity; however, it does this without having to track all individuals as would a more computationally expensive IBM.

Due to this simplicity, the model does not focus on just one population with one trait (Loeuille and Loreau, 2005), but attempts to model a multispecies system. I do this by introducing feedback between ecological traits and the abiotic environment (chapter 4), as well as via feedbacks between species, as done in several other multispecies or foodweb models (Brännström et al., 2012; Allhoff and Drossel, 2013). While, my model does not take into account spatial structure such as (Fronhofer and Altermatt, 2015; Kubisch et al., 2016), it does have size structure, which is important when looking at species with indeterminate growth, such as teleosts, that can vary in size over several orders of magnitude through their lifetime. This variation and the consequent central role of size in ecosystem structuring observed in real world marine systems, Jennings and Collingridge 2015; Blanchard et al. 2017a could be more important than a spatial structure, at least for pelagic ecosystems. A next step for eco-evolutionary dynamics studies would be to develop mechanistic models tracking the dynamics of phenotypic and genotypic variations in populations using contemporary evolution but over timescales of tens to hundreds of generations (Govaert et al., 2019) and potentially on richer spatial domains. Our model thus fits in with other eco-evolutionary models not as the ultimate solution but as a first step of a size-structured mechanistic model tracking phenotypic diversity over longer periods of time. The next step for such a model would be to incorporate the heritability of traits within species. This approach has been widely used in size-structured integral projection models, where size is a continuous trait and models are typically parameterised from very detailed individual level data for populations or small sets of species (Rees and Ellner, 2016). To better capture evolutionary processes in a way that reflects whole ecosystems taking this approach will be challenging. The ultimate achievement would be to close the gap between theory and observations, to be able to verify the

hypothesis we tested and to ensure the outcomes of further model development reflects nature (Rueffler et al., 2006).

5.5 Wider applications for biodiversity research and future extensions

There is now considerable scope to further explore eco-evolutionary dynamics using MizerEvolution. For example, by adding adaptive traits and appropriate trade-offs, or new traits such as the shape of feeding kernel, predator search rate, maximum size, or metabolic speed/allocation, the model provides the mechanism by which I can explore the link between environmental changes.

An example of this would be invasive species. My research so far focused on adaptation within species, which lead to changes in ecosystem function and structure. One anthropomorphic disturbance that is not covered in this thesis is the concept of invasive species or species redistributions (Pecl et al., 2017). These invasions act similarly to the introduction of new phenotypes in an ecosystem, albeit on a much greater scale, as interspecific differences between invading and endemic species are typically greater than intraspecific differences among phenotypes. Exploring these invasions will help address a range of research questions, including: (1) the influence of these invasions on the adaptation of local species adaptation (Ricciardi and Atkinson, 2004); (2) identification of the range of factors that determine the success of an invasion; and (3) how the dynamics of truly novel species invasions or introductions differ (or not) to the effects of range extending species on ecosystem functioning (Robinson et al., 2019). Food web models such as Ecopath with Ecosim (Christensen and Walters, 2004) or Atlantis (Audzijonyte et al., 2019) have been used to tackle invasion issues (Downing et al., 2012; Kao et al., 2014; Nyamweya et al., 2016), but to our knowledge, no food web model has been able to study the invasion of one or several species on a food web which can adapt to the changes caused by the invasion (Corrales et al., 2020).

5.6 Conclusions

The model developed in this thesis, puts trait-based size-spectrum models into the mix of emerging eco-evolutionary models. Its mechanistic approach allows it to model complex size-structured evolutionary food-webs through time, yielding emerging interactions among and within species along with their adaptation patterns. The model managed to reproduce evolutionary trends from well-studied fish populations and communities, while also introducing new knowledge on the effects of multi-species interactions and size-structured species on adaptation of various traits. Hopefully, this is a first step towards bringing the trait-based size-structured modelling approach closer to natural evolving ecosystems.

Appendix A

Sensitivity analysis for chapter 2

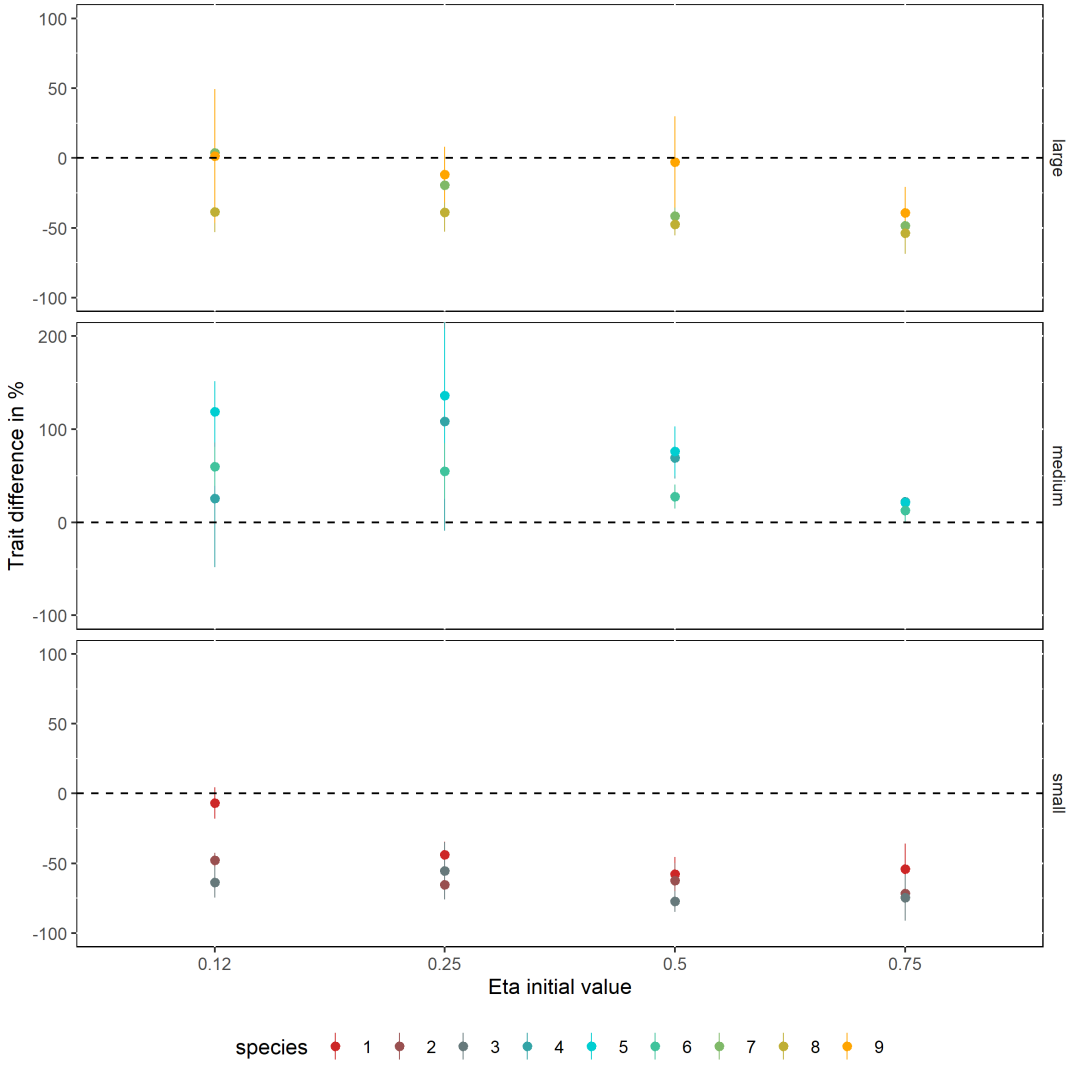
The robustness of our model outcomes to parameter assumptions was explored in an extensive set of simulations. In these sensitivity analyses we are mostly looking at the qualitative difference in results, i.e. whether the direction of evolutionary change in maturation size (up or down from the initial value) is the same as in the baseline scenarios. We are less concerned about the absolute quantitative change. Changing the initial η (Fig.S.1) resulted in different final η values for some of the medium-sized species and, to a lesser extent, the large species, but the range of values we explored led to qualitatively similar trait changes by the end of the simulation and did not affect our overall conclusions. Regardless of the initial values of η, by the end of the 3000 years, they all declined in small bodied species, and mostly increased in the middle sized species.

We assessed whether our assumptions about key predation parameters – predator-prey mass ratio (β) and width of predation kernel (σ) - affected the direction (increase or decrease) in maturation size change at the end of 6000-year simulation period. We found that, although the magnitude of the change varied somewhat, for all species the direction of evolutionary trends were generally the same as in the baseline scenario. The only exception was for the highly variable species 4 and especially 5, when β or σ values were very small (50 and 0.9 respectively) (Figs.S.6,S.5).

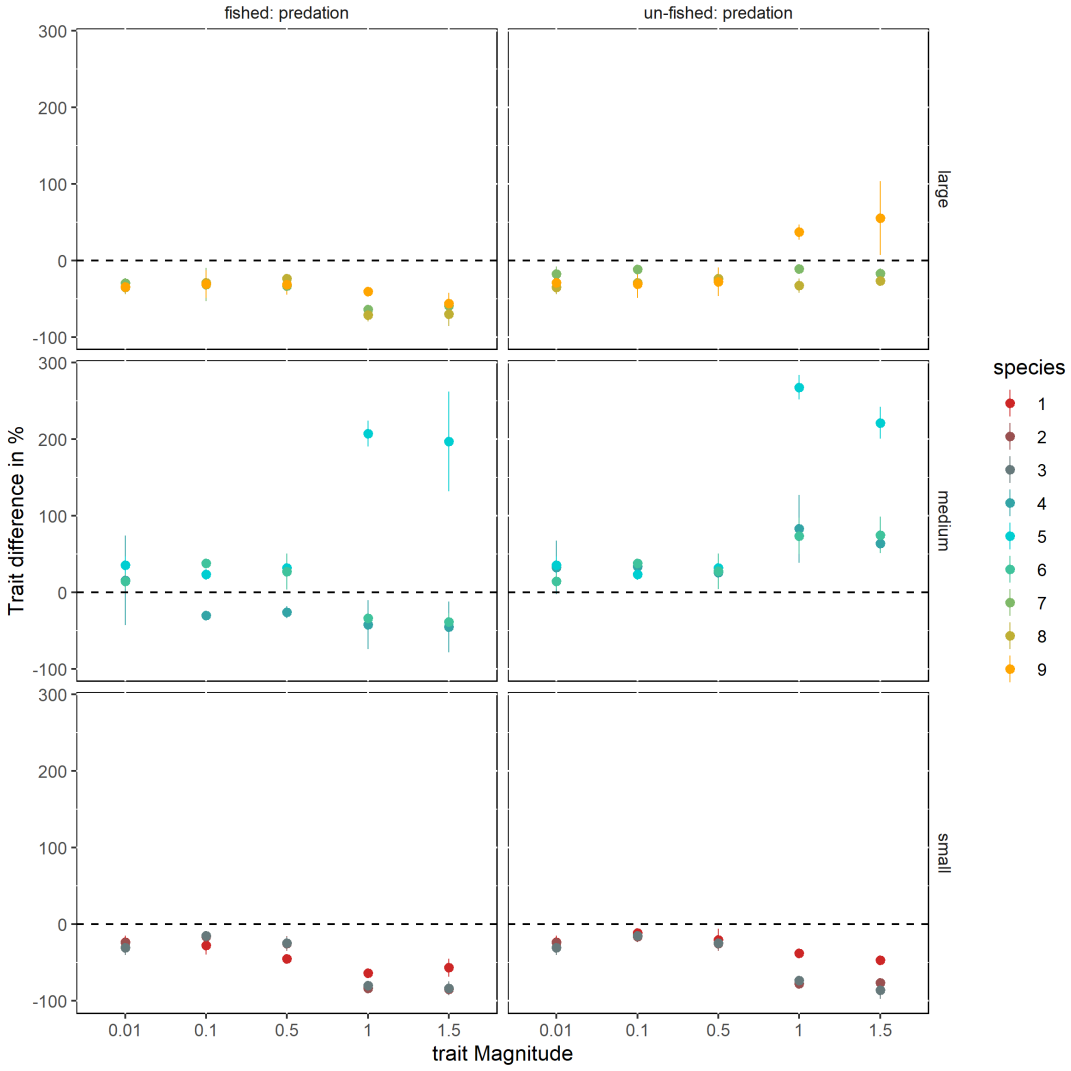
Next, we explored sensitivity of model output to four parameters determining the rate of evolution: the magnitude of trait change, the phenotype appearance rate (χ) and the phenotype abundance upon introduction. The rate at which new phenotypes were introduced (χ) affected

the speed of evolution, and almost no evolution occurred when the rate was 10 to 100 times slower than in the main simulation set (Fig.S.3). Yet, a 50% increase in χ gave qualitatively similar responses to fishing. Similarly, the magnitude of change between new and parent phenotypes determined the rate of evolution, where large amplitude of changes led to faster evolution, yet the qualitative response to fishing remained the same (Fig.S.2). Similarly, changing the initial abundance of a new phenotype along a continuum from 0.01% to 10% of the parent's abundance led to very similar evolutionary responses to those reported in the main text.

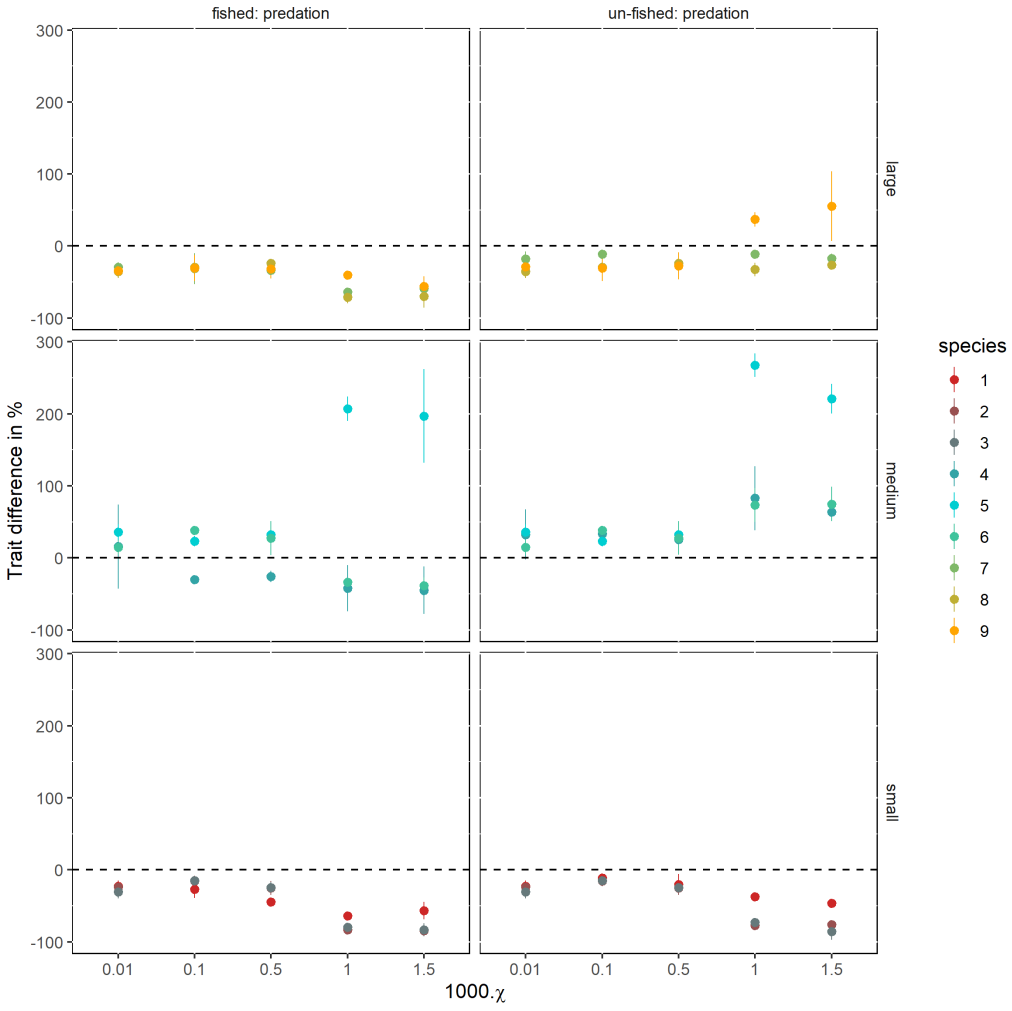
Finally, increasing the number of replications per scenario from 10 to 50 (in the scenario with predation and fishing) did not strongly affect the observed variation and demonstrated that 10 replications were largely sufficient to capture the variation and trends in trait evolution; the size of standard deviation bars remains the same across different replication values (Figs.S.7,S.8).



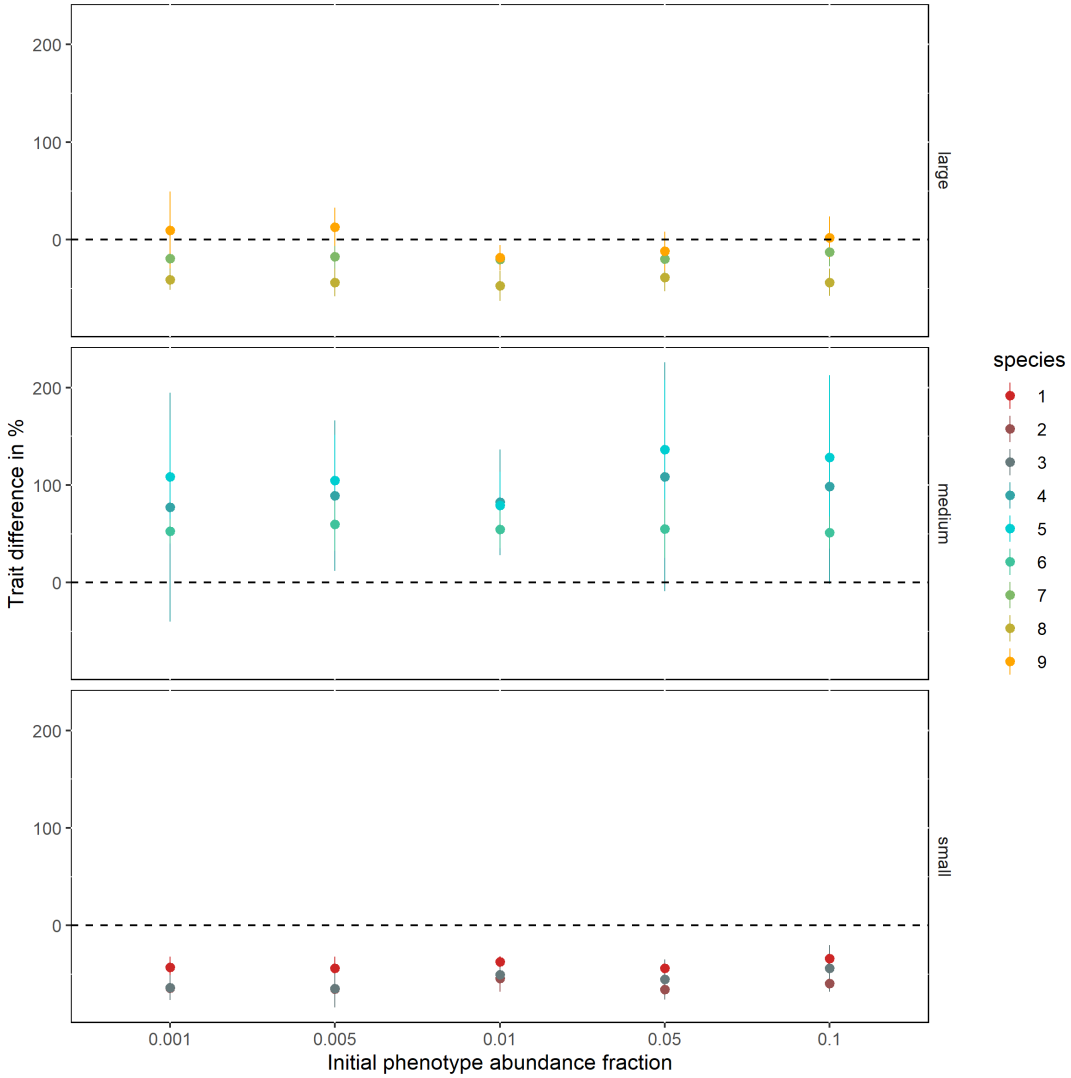
SUPPLEMENTARY FIGURE S.1: Effect of varying the initial η value on the evolution of trait value at the end of 3000 year simulation before fishing is started. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.25. Sensitivity analysis shows that the overall direction of trait change (up or down from the dashed line) remains similar across the range of initial η values



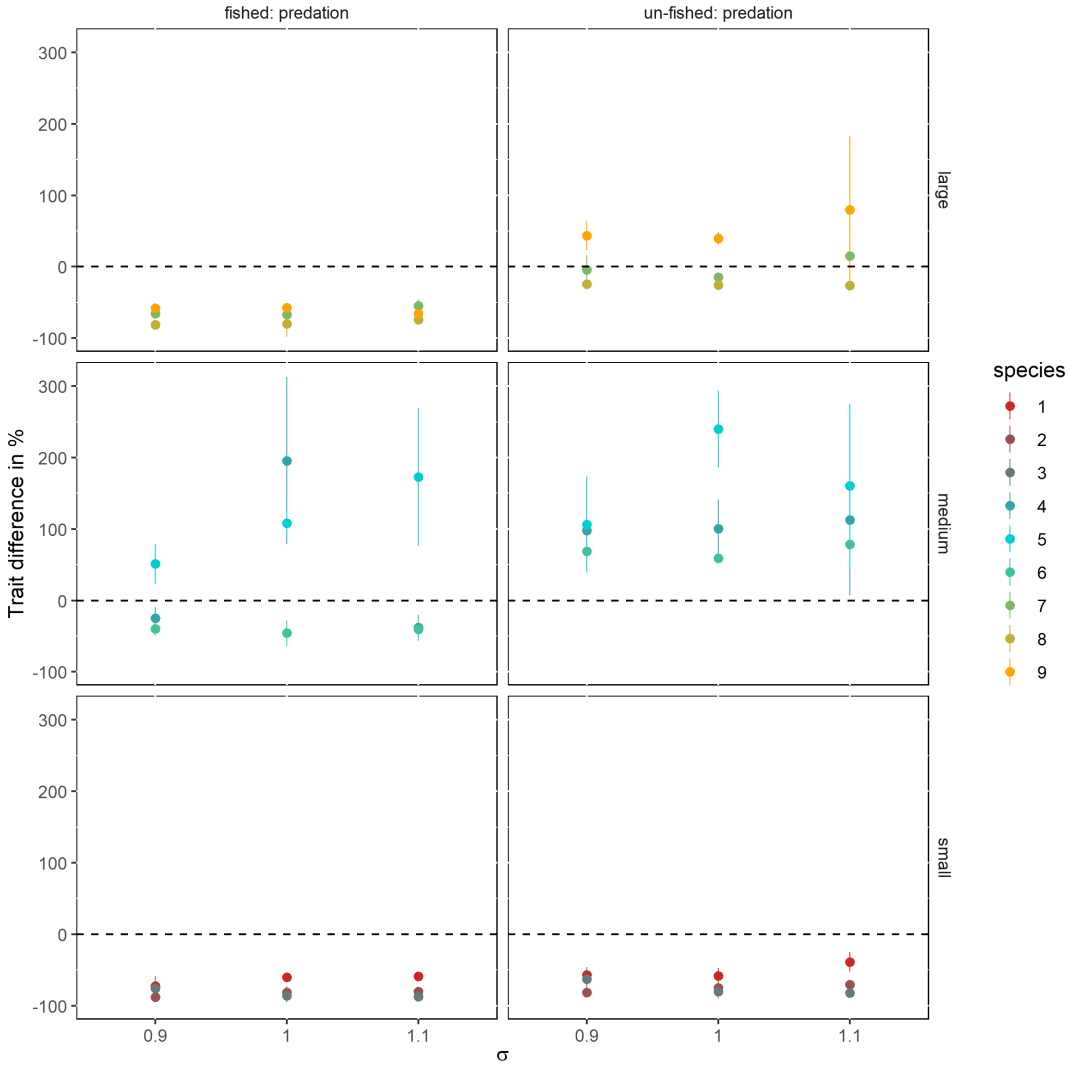
SUPPLEMENTARY FIGURE S.2: Effect of varying the magnitude of the trait evolution after 6000 years. The trait magnitude determines the maximum percentage difference possible between parent and new trait's phenotype. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.2.



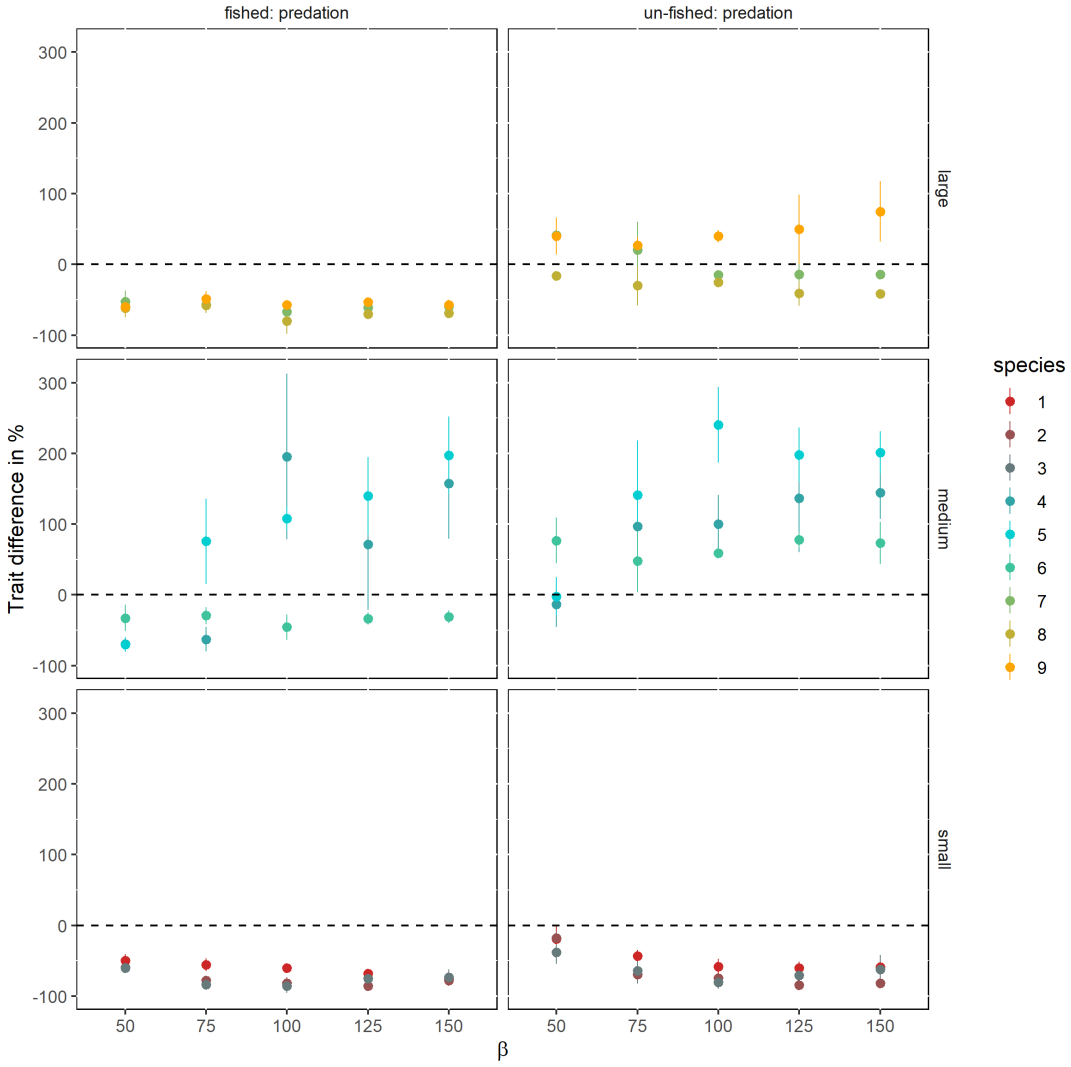
SUPPLEMENTARY FIGURE S.3: Effect of varying the χ parameter on the trait evolution after 6000 years. The χ parameters determines the probability of new phenotype appearance. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.001.



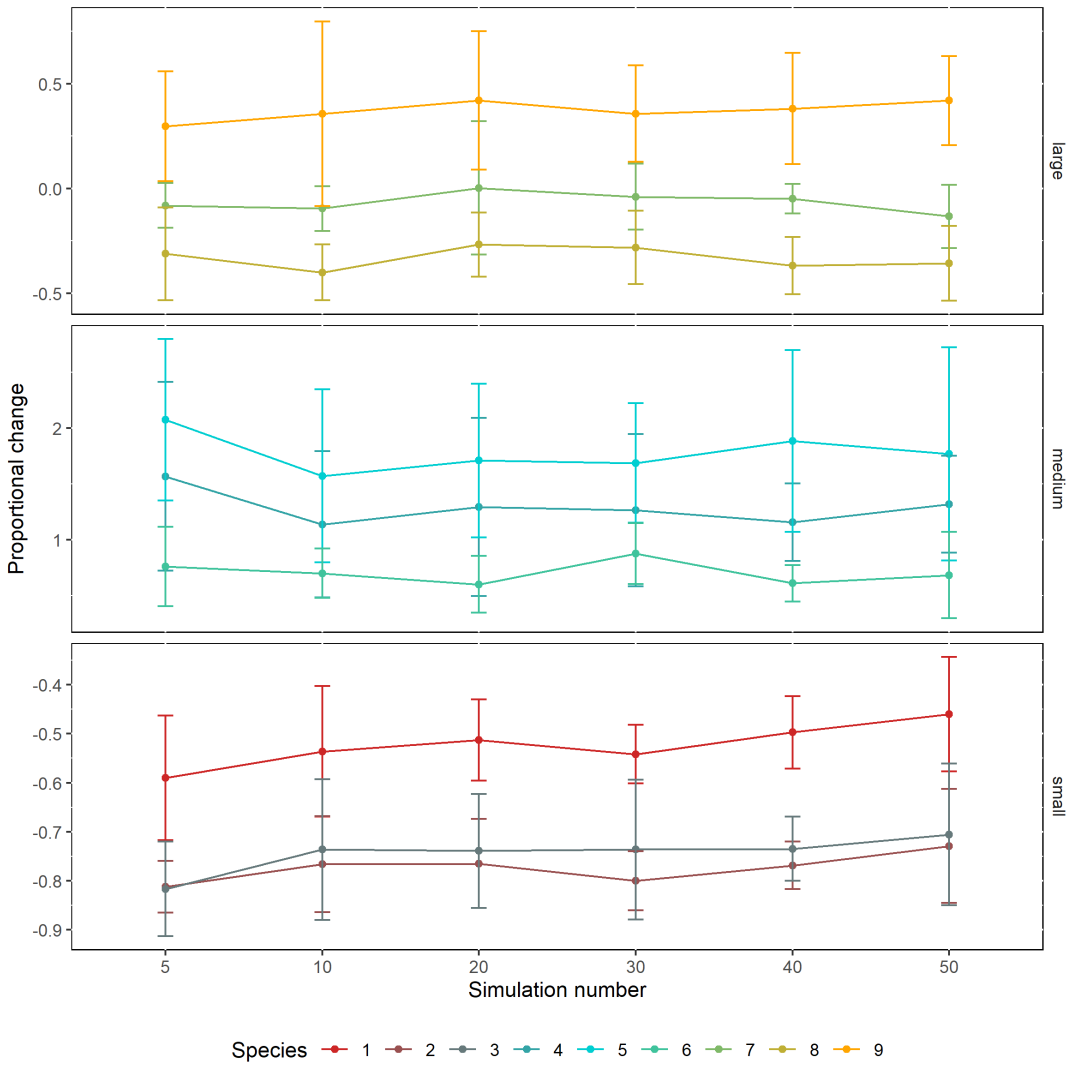
Supplementary Figure S.4: Effect of varying the initial phenotype abundance upon introduction at the end of 3000 year simulation before fishing is started. This parameter determines what fraction of a parent's biomass is used as an initial biomass for new phenotypes. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.05.



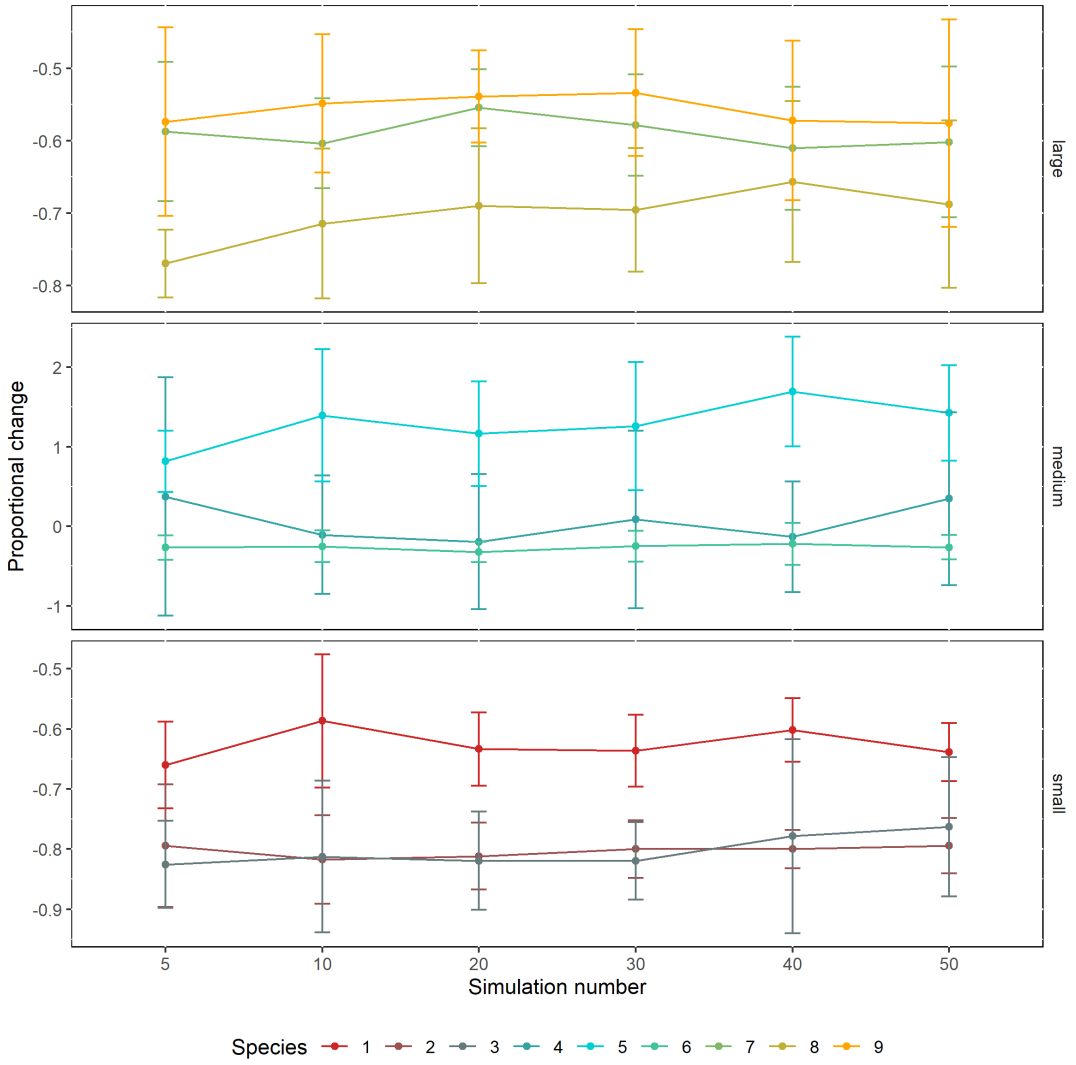
SUPPLEMENTARY FIGURE S.5: Effect of varying the σ parameter on the trait evolution after 6000 years. The σ parameter determines the width of the feeding kernel. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 1.



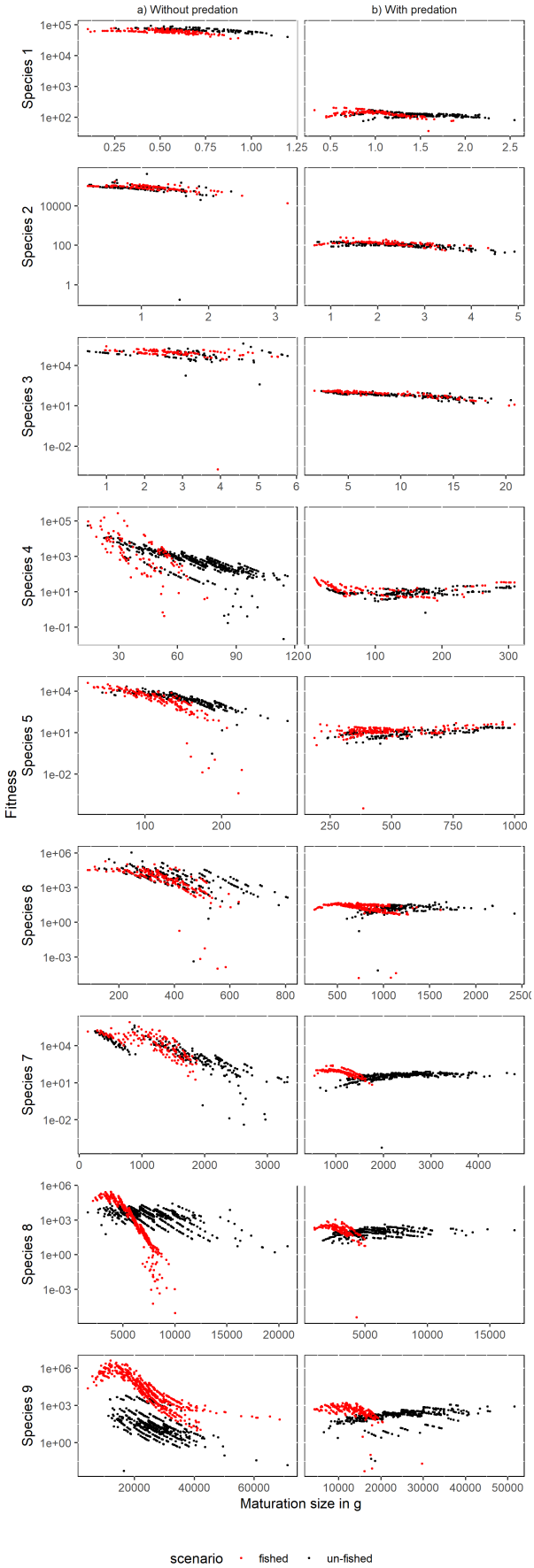
SUPPLEMENTARY FIGURE S.6: Effect of varying the β parameter on the trait evolution after 6000 years. The β parameter determines the preferred predator-prey mass ratio. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 100.



SUPPLEMENTARY FIGURE S.7: Effect of increasing number of simulations on the patterns of trait evolution in simulations without fishing (year 6000). The trait's value per species are plotted against the number of simulations to determine the minimum number of runs necessary to have robust results. Error bars show the standard deviation of the results, demonstrating that variation across simulations is captured sufficiently well with 10 replications used in the main analyses.



SUPPLEMENTARY FIGURE S.8: Effect of increasing number of simulations on the patterns of trait evolution in simulations with fishing (year 6000). For other details see legend of Fig.S.7.



SUPPLEMENTARY FIGURE S.9: Species' fitness across simulations. Each dot shows fitness of a phenotype with different maturation size in scenarios with (red) and without (black) fishing across simulations. The figure shows phenotypes in a cohort starting at year 5500 in simulations without (a) and with (b) predation.

Appendix B

Supplementary information for chapter 2

SUPPLEMENTARY TABLE S.1: Model selection table. df is degrees of freedom; logLik is likelihood; AICc is Akaike information criterion; delta is change in AICc. fsh - fishing, prd - predation, sp - species (all treated as factors). The best model is on the top row and includes all factors and their interactions. The second best model (second row) does not include the three-way interaction.

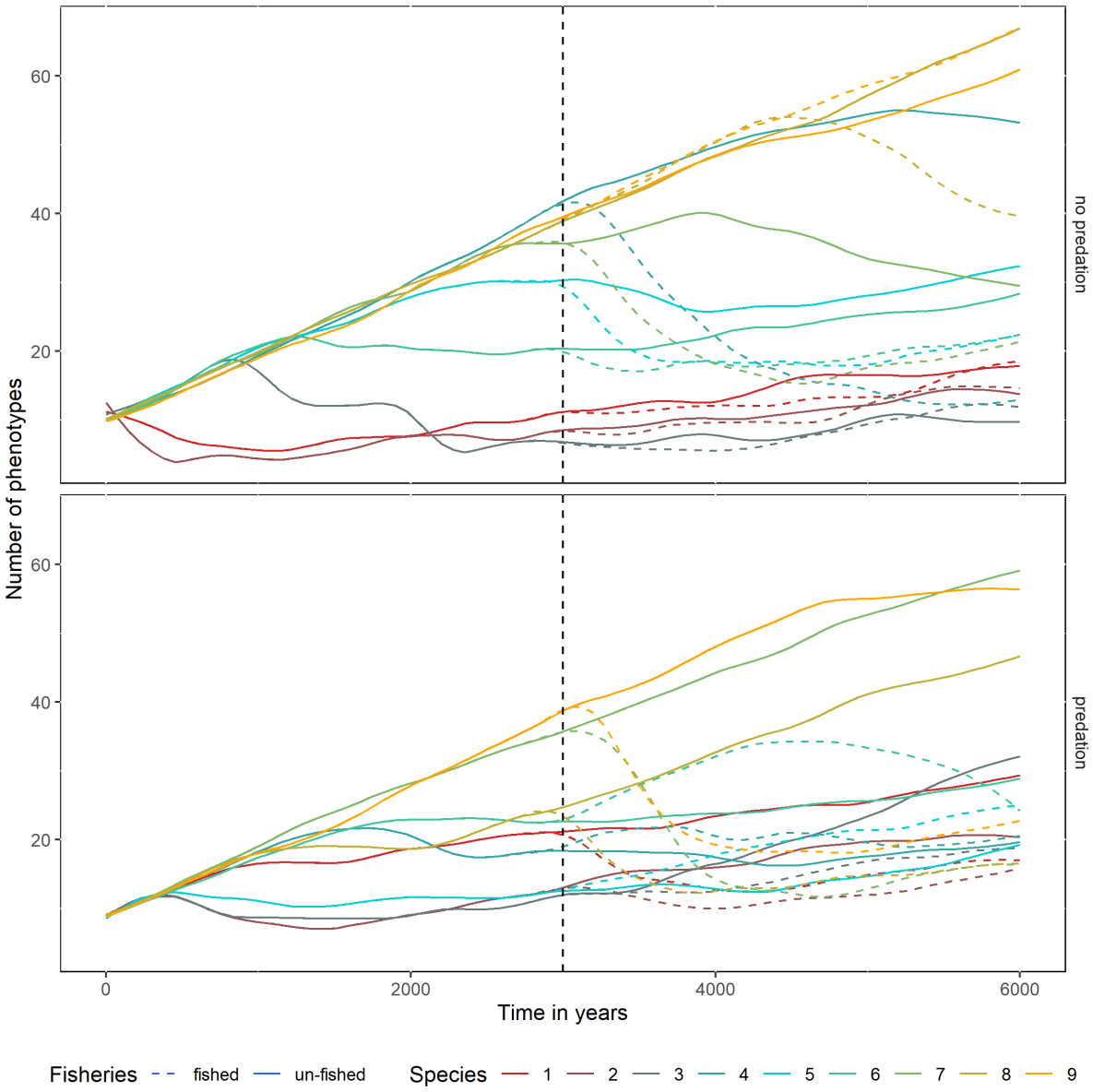
	(Intercept)	fsh	prd	sp	fsh:prd	fsh:sp	prd:sp	f:p:s	df	logLik	AICc	delta
128	-3.2	+	+	+	+	+	+	+	37	-147.38	377.49	0
64	-3.12	+	+	+	+	+	+		29	-158.61	380.5	3.01
56	-3.19	+	+	+		+	+		28	-164.83	390.57	13.08
48	-3.29	+	+	+	+		+		21	-190.11	424.96	47.47
40	-3.36	+	+	+			+		20	-195.35	433.18	55.69
39	-3.13		+	+			+		19	-241.79	523.82	146.33
32	-3.02	+	+	+	+	+			21	-274.09	592.91	215.42
24	-3.09	+	+	+		+			20	-277.39	597.26	219.77
16	-3.19	+	+	+	+				13	-291.36	609.77	232.28
8	-3.26	+	+	+					12	-294.36	613.62	236.13

SUPPLEMENTARY TABLE S.2: ANOVA table for the 3-way model $log(\eta)$ Species*Predation*Fishing. Partial effects sizes for each term are also reported (pes). Model is the first line of table S.1

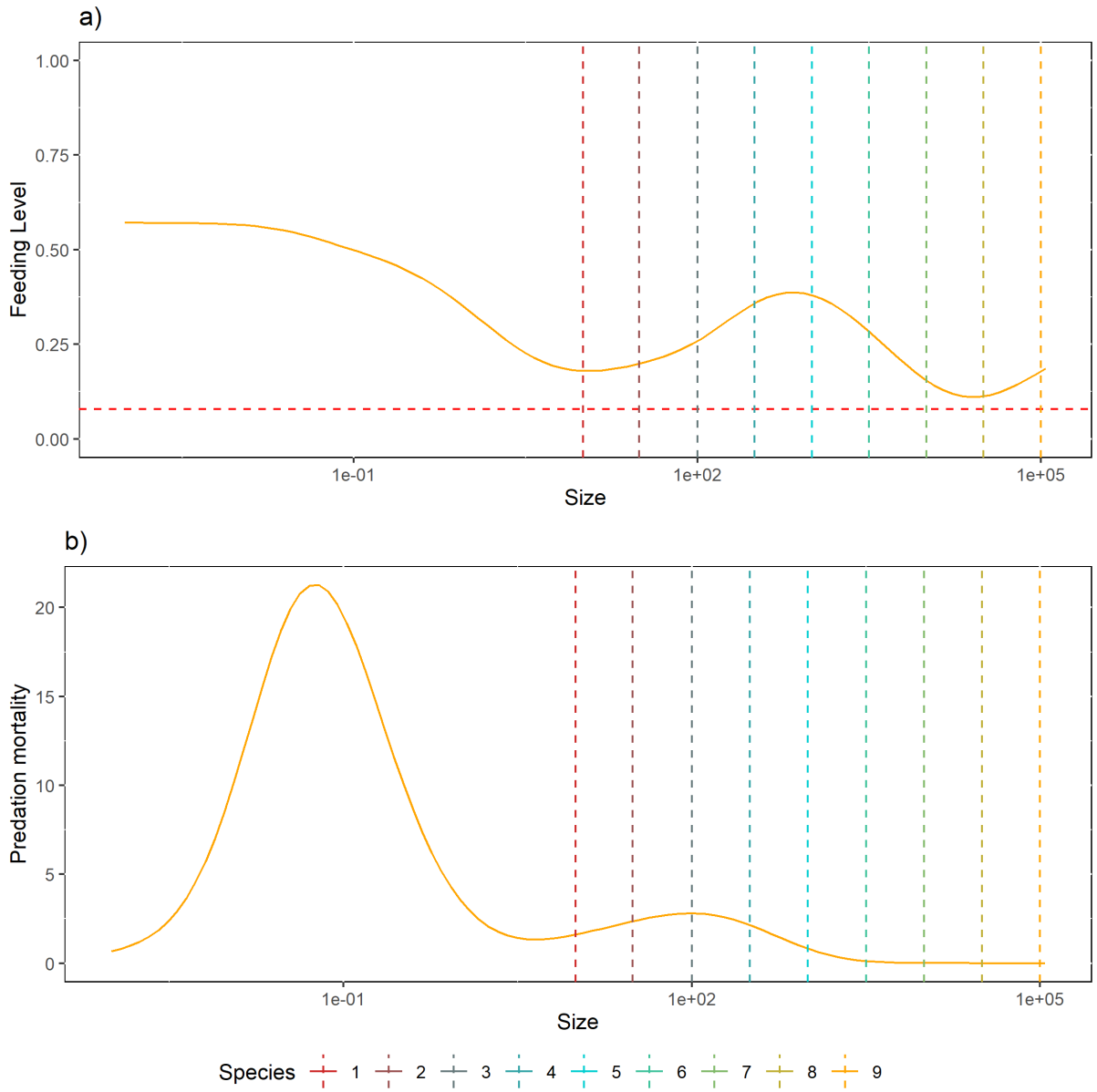
	Df	Sum Sq	Mean Sq	F value	Pr(>F)	pes
species	8	190.27	23.78	161.22	0	0.79
predation	1	42.14	42.14	285.65	0	0.46
fisheries	1	18.36	18.36	124.5	0	0.27
species:predation	8	45.75	5.72	38.77	0	0.48
species:fisheries	8	9.73	1.21	8.24	0	0.16
predation:fisheries	1	1.78	1.78	12.12	0	0.03
species:predation:fisheries	8	3.07	0.38	2.6	0.01	0.06
Residuals	324	47.79	0.14	NA	NA	NA

SUPPLEMENTARY TABLE S.3: Empirical size data and their references used in Fig.2.6

Species	Maturation size	Asymptotic size	References
Cod	3337.375666	19428.63866	Jennings et al. 1998
Haddock	334.656743	3117.98674	Jennings et al. 1998
Herring	111.102066	221.41796	Goodwin et al. 2006
Norway pout	46.924711	86.11638	Jennings et al. 1998
Plaice	203.236035	1496.00467	Jennings et al. 1998
Saithe	1459.741393	45627.15377	Jennings et al. 1998
Sandeel	3.563648	34.52603	Goodwin et al. 2006
Sole	150.154812	684.44291	Jennings et al. 1998
Sprat	15.674781	32.24996	Bailey 1980
Whiting	60.689	612.10952	Jennings et al. 1998
Dab	21.712738	211.24228	Rijnsdorp et al. 1992
Grey Gurnard	103.313363	886.01239	Fishbase
Anoplopoma fimbria	2243.365824	3388.987552	Olsson and Gislason, 2016
Anoplopoma fimbria	2495.410527	2591.429307	Olsson and Gislason, 2016
Sebastes crameri	839.2709096	1623.941784	Olsson and Gislason, 2016
Sebastes elongatus	114.0872975	727.4969882	Olsson and Gislason, 2016
Sebastes flavidus	1159.479145	2013.986983	Olsson and Gislason, 2016
Clupea harengus	144.4055108	234.7223797	Olsson and Gislason, 2016
Clupea harengus	152.5260593	306.5630249	Olsson and Gislason, 2016
Clupea harengus	127.5720137	219.7998486	Olsson and Gislason, 2016
Clupea harengus	215.6687028	367.248827	Olsson and Gislason, 2016
Clupea harengus	122.5440299	245.7383233	Olsson and Gislason, 2016
Clupea harengus	236.954886	382.5939548	Olsson and Gislason, 2016
Clupea harengus	240.5513444	330.4041016	Olsson and Gislason, 2016
Clupea pallasi	120.1927067	215.8984944	Olsson and Gislason, 2016
Clupea pallasi	173.2437888	453.506854	Olsson and Gislason, 2016
Clupea pallasi	66.6359996	215.8984944	Olsson and Gislason, 2016
Gadus macrocephalus	1448.78265	11769.19016	Olsson and Gislason, 2016
Gadus morhua	5825.230626	22718.35315	Olsson and Gislason, 2016
Gadus morhua	3472.860386	20086.52614	Olsson and Gislason, 2016
Gadus morhua	2288.576711	10111.50945	Olsson and Gislason, 2016
Gadus morhua	2021.927647	3262.315803	Olsson and Gislason, 2016
Gadus morhua	1190.137173	1645.589879	Olsson and Gislason, 2016
Gadus morhua	1768.349977	14147.75821	Olsson and Gislason, 2016
Melanogrammus aeglefinus	293.170736	3279.323679	Olsson and Gislason, 2016
Melanogrammus aeglefinus	698.1900651	2630.904545	Olsson and Gislason, 2016
Melanogrammus aeglefinus	707.9575712	3834.294493	Olsson and Gislason, 2016
Merlangius merlangus	179.256487	1495.422983	Olsson and Gislason, 2016
Merlangius merlangus	62.34150354	620.9007471	Olsson and Gislason, 2016
Theragra chalcogramma	294.78	3014.60454	Olsson and Gislason, 2016
Theragra chalcogramma	379.8975	730.02	Olsson and Gislason, 2016
Theragra chalcogramma	555.66	1509.22542	Olsson and Gislason, 2016
Trisopterus esmarkii	42.4700496	76.1849616	Olsson and Gislason, 2016
Hippoglossoides platessoides	878.5564359	5363.615599	Olsson and Gislason, 2016
Pleuronectes ferruginae	231.7439325	623.8158895	Olsson and Gislason, 2016
Pleuronectes ferruginae	141.712941	706.969943	Olsson and Gislason, 2016
Pleuronectes platessa	251.4994817	2287.908563	Olsson and Gislason, 2016
Pleuronectes platessa	188.4555558	1049.062573	Olsson and Gislason, 2016
Pleuronectes platessa	197.3690262	1749.712324	Olsson and Gislason, 2016
Solea solea	134.6253253	1233.978732	Olsson and Gislason, 2016
Solea solea	145.1377053	591.8365986	Olsson and Gislason, 2016
Carcharhinus brevipinna	57578.96575	178213.8916	Olsson and Gislason, 2016
Carcharhinus falciformis	79173.44259	181720.6787	Olsson and Gislason, 2016
Carcharhinus isodon	8814.472849	18111.37362	Olsson and Gislason, 2016
Carcharhinus limbatus	15063.79472	26326.34765	Olsson and Gislason, 2016
Carcharhinus sorrah	8153.456825	22868.00295	Olsson and Gislason, 2016
Carcharhinus sorrah	4704.774274	11108.36879	Olsson and Gislason, 2016
Carcharhinus tilstoni	11054.41718	48226.29158	Olsson and Gislason, 2016
Galeorhinus galeus	13556.40429	23279.53846	Olsson and Gislason, 2016
Mustelus antarcticus	5515.412778	37633.86675	Olsson and Gislason, 2016
Mustelus antarcticus	5840.80978	48712.8062	Olsson and Gislason, 2016
Prionace glauca	203867.6355	371380.9422	Olsson and Gislason, 2016
Menidia menidia	2.3	9.3	Conover and Munch, 2002
Menidia menidia	3.8	10	Conover and Munch, 2002
Menidia menidia	5.2	10.5	Conover and Munch, 2002
Poecilia reticulata	0.0761	0.590746429	Reznik et al., 1997
Poecilia reticulata	0.0675	0.590746429	Reznik et al., 1997
Poecilia reticulata	0.1892	3.602635961	Reznik et al., 1997
Poecilia reticulata	0.1623	3.602635961	Reznik et al., 1997
Danio rerio	0.0749	0.2134	Ulloa et al., 2011



SUPPLEMENTARY FIGURE S.1: Number of phenotypes through time per species averaged across all stochastic realisations. The vertical line shows the introduction of fisheries and the dashed line shows phenotype numbers in simulations with fishing.



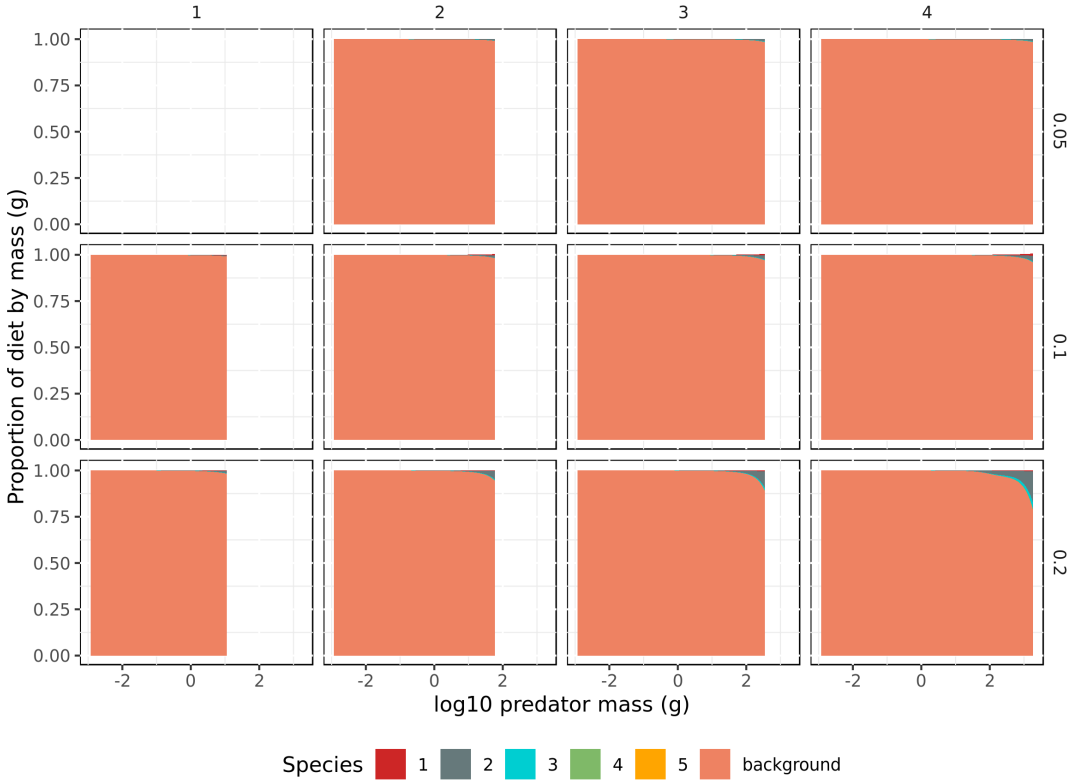
SUPPLEMENTARY FIGURE S.2: Feeding level and predation mortality through sizes for one un-fished stochastic simulation after 6000 years of evolution. Parameters that determine feeding and predation are the same between species so their profiles overlap. The vertical dashed lines show the asymptotic size of each species. a) shows the feeding level, where 1 is the maximum feeding level defined by the maximum intake rate. The horizontal red line indicate the critical feeding level, below which starvation mortality applies. b) shows the instantaneous predation mortality value.

Appendix C

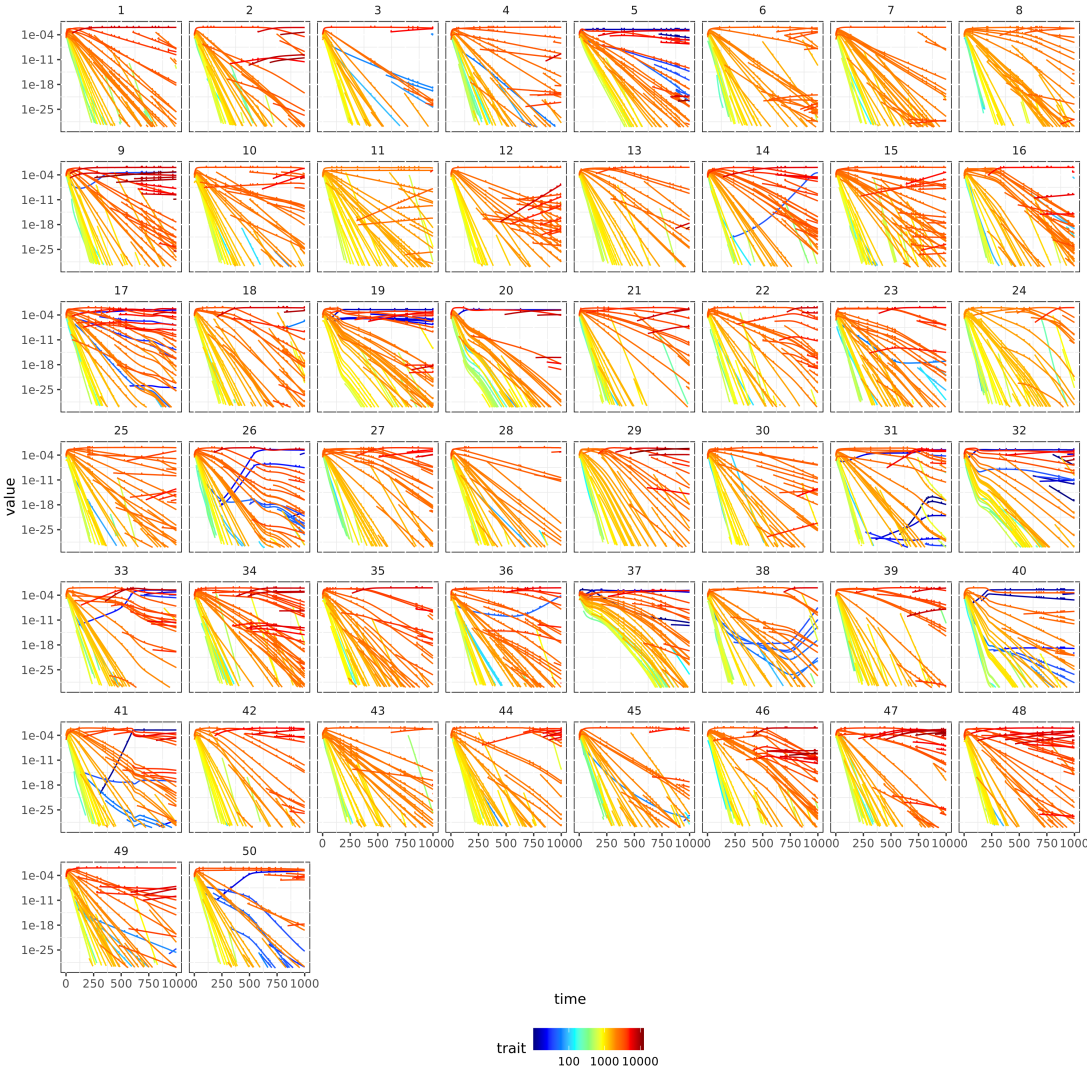
Supplementary material for chapter 3

SUPPLEMENTARY TABLE S.1: Values of x and y determining the trade-off relationship between α and β

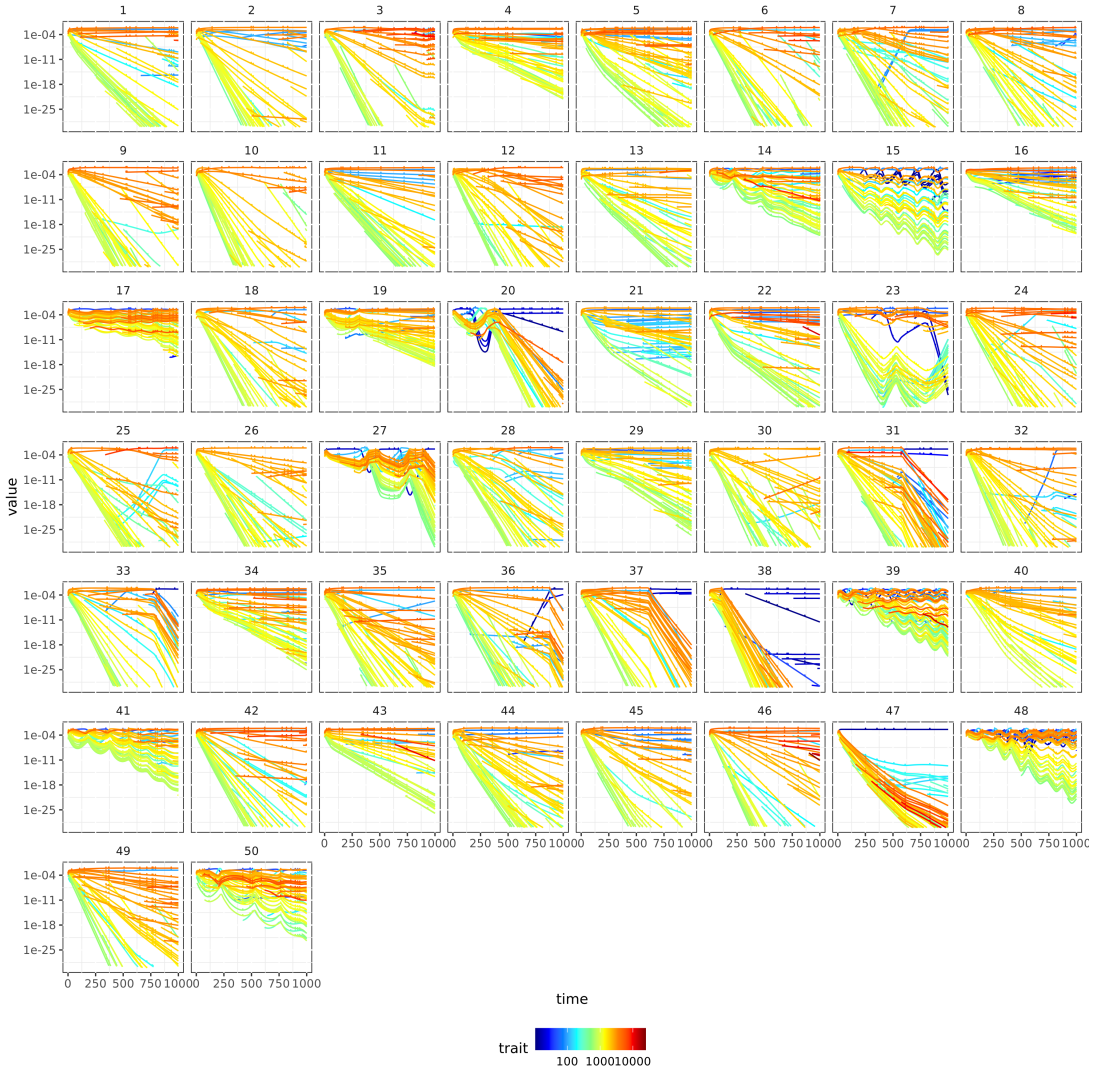
X	Y	Color in Fig.3.4
3	1	Red
6	3	Yellow
4	3	Green
3.5	1.1	Blue
1.5	0	Purple



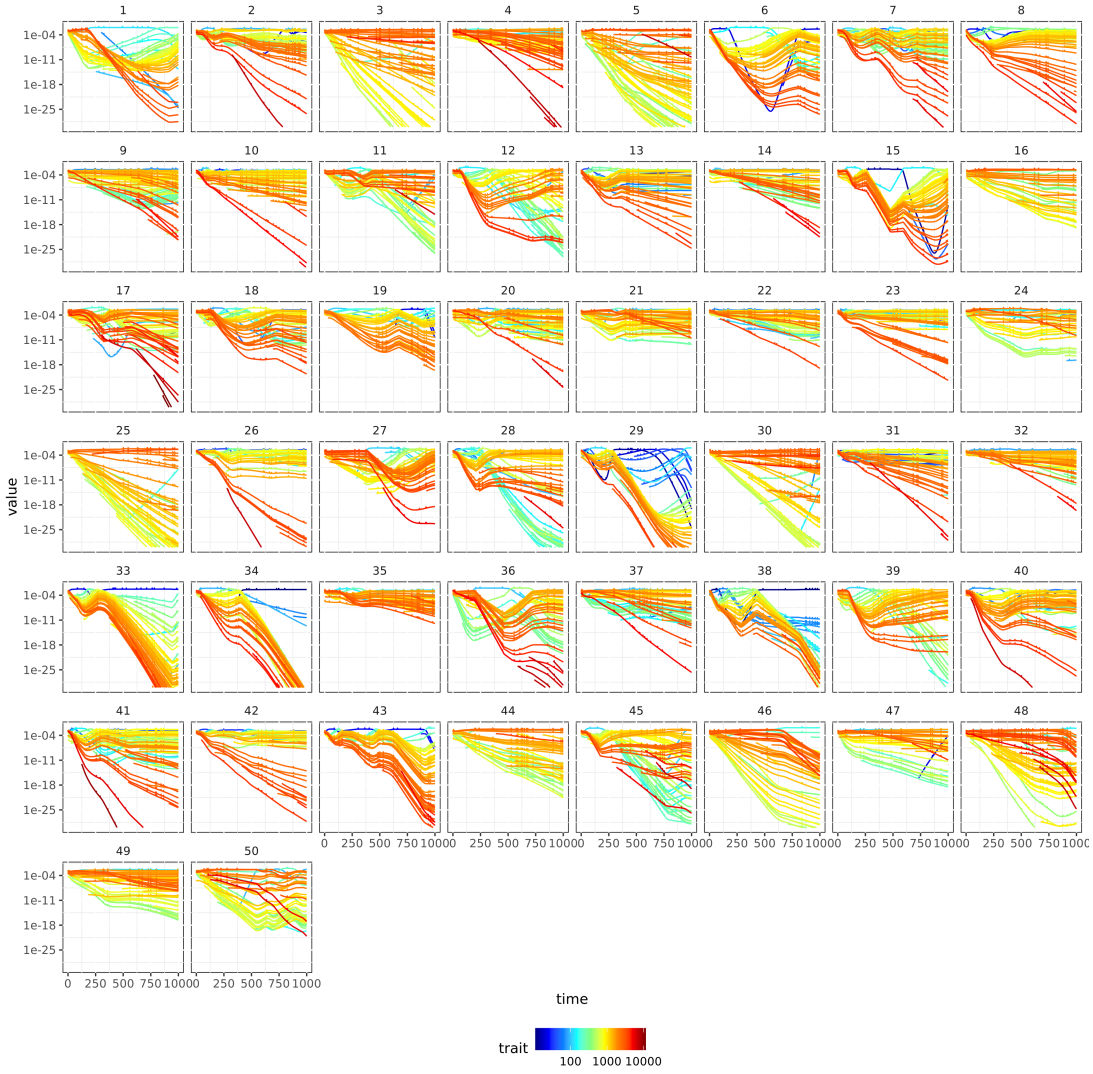
SUPPLEMENTARY FIGURE S.1: Diet composition of the 4 smallest species in the community per resource availability. There is no diet for species 1 at $\kappa = 0.05$ as it was not able to survive under such conditions.



SUPPLEMENTARY FIGURE S.2: Biomass of phenotypes through time according to their trait value. Each panel is a simulation showing the biomass of the different phenotypes composing species 5. The color indicates the PPMR value, blue is low value and therefore shows a "piscivore" phenotype while red is "planktivory". These simulations have a κ of 0.05 (low resource availability).



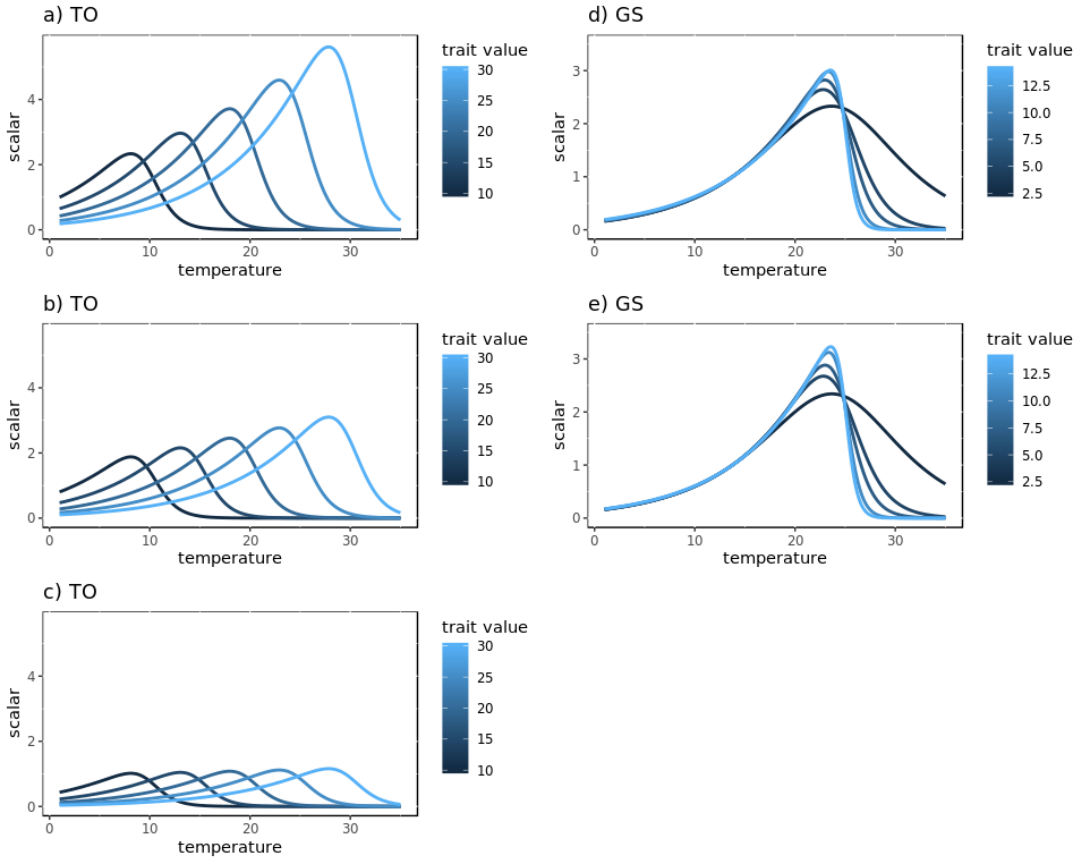
SUPPLEMENTARY FIGURE S.3: Biomass of phenotypes through time according to their trait value. Each panel is a simulation showing the biomass of the different phenotypes composing species 5. The color indicates the PPMR value, blue is low value and therefore shows a "piscivore" phenotype while red is "planktivory". These simulations have a κ of 0.1 (medium resource availability).



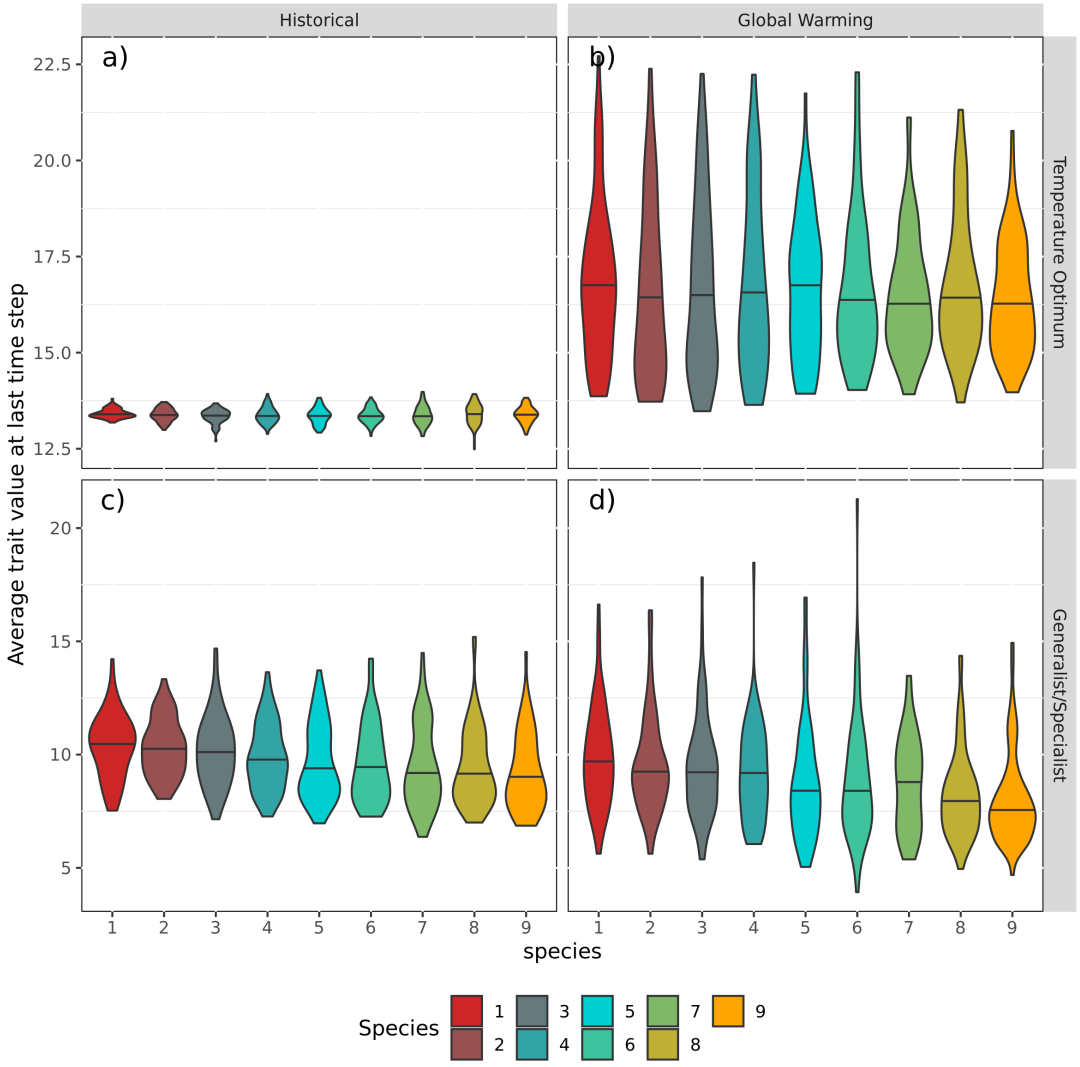
SUPPLEMENTARY FIGURE S.4: Biomass of phenotypes through time according to their trait value. Each panel is a simulation showing the biomass of the different phenotypes composing species 5. The color indicates the PPMR value, blue is low value and therefore shows a "piscivore" phenotype while red is "planktivory". These simulations have a κ of 0.2 (high resource availability).

Appendix D

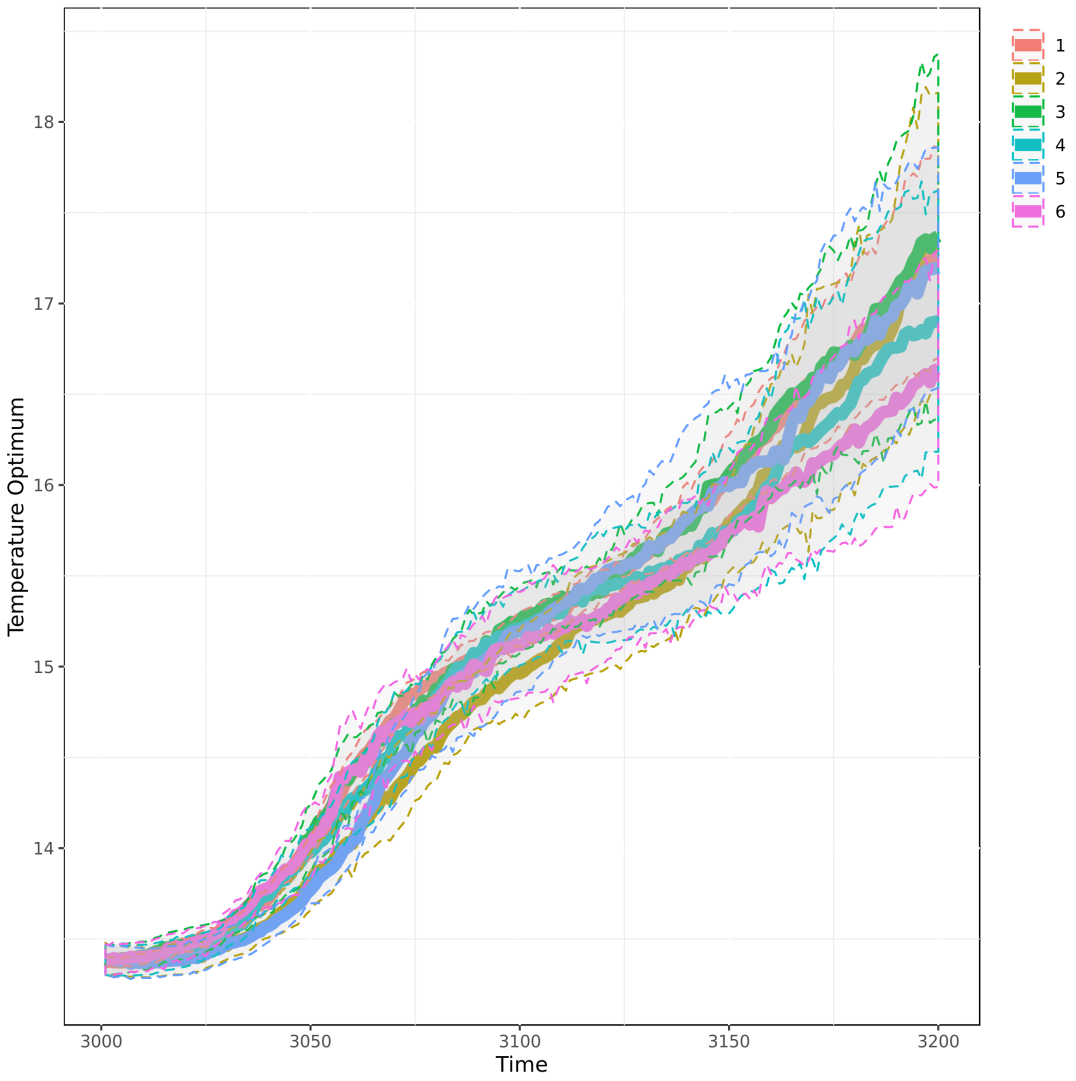
Supplementary material for chapter 4



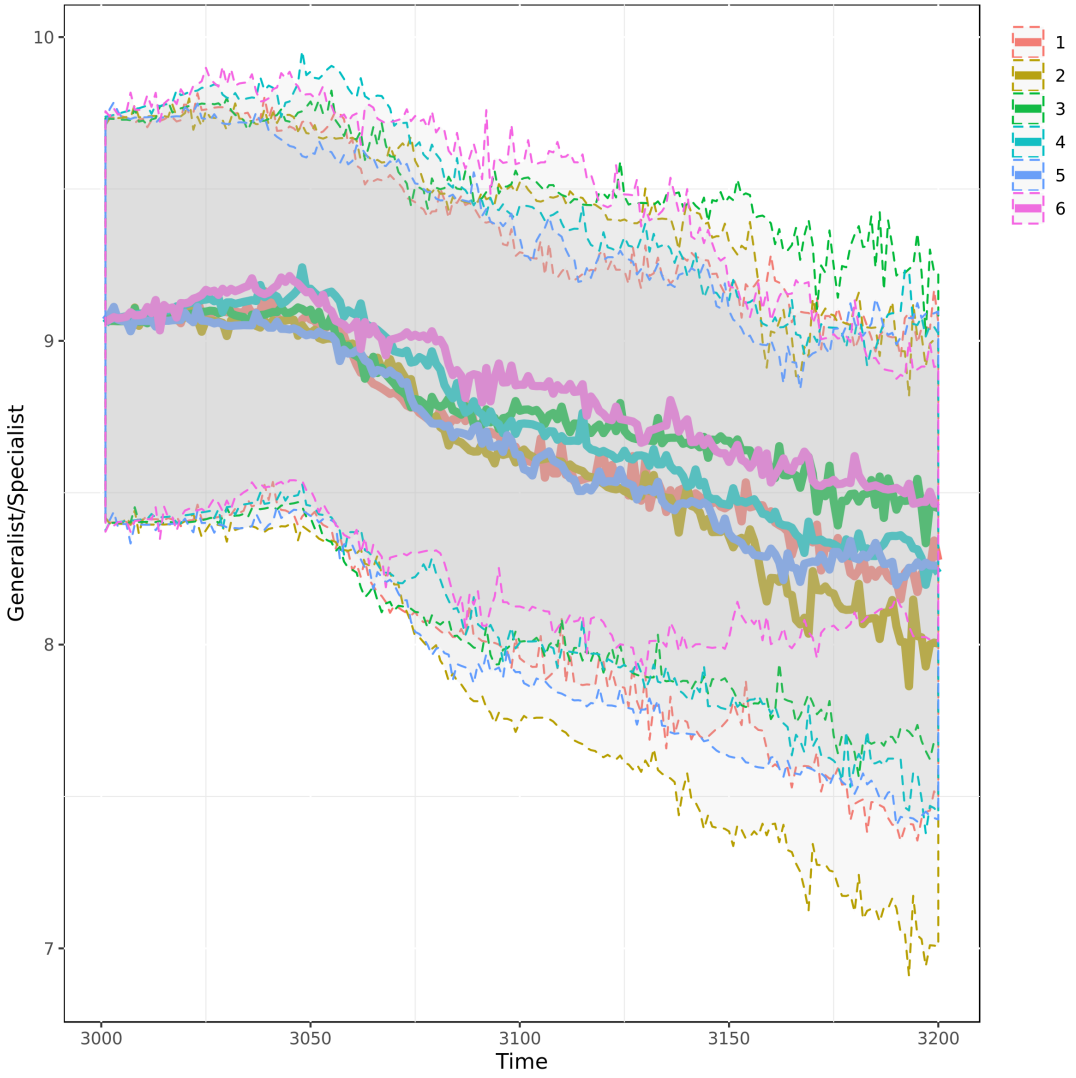
SUPPLEMENTARY FIGURE S.1: Multiple trade-offs were tested between the thermal performance traits, shown in this figure. This study uses a combination of b) for TO and d) for GS, which we will call scenario 1. 5 other scenarios were explored and are detailed below. 2 is a and d); 3 is c and d); 4 is b and e); 5 is a and e); 6 is c and e).



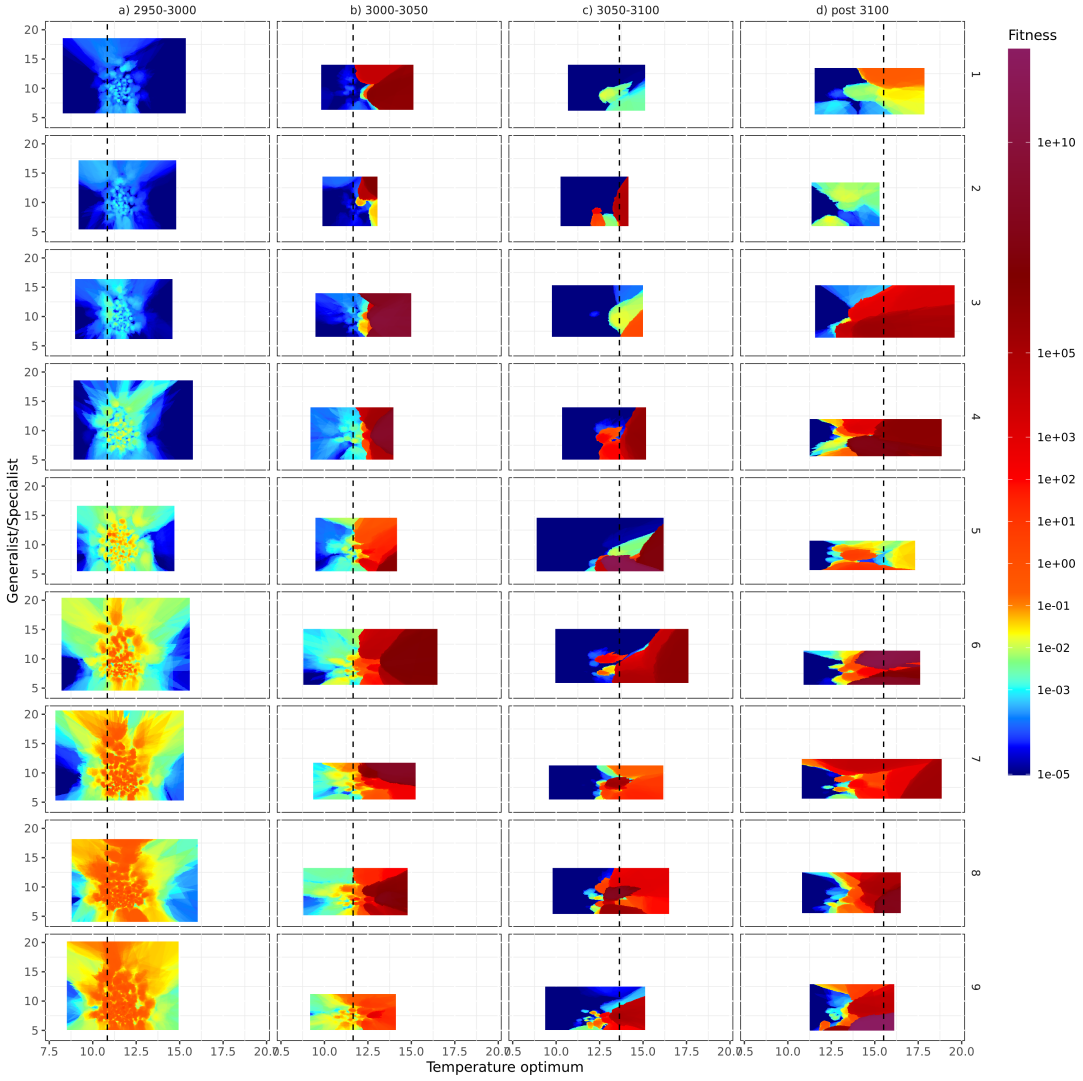
Supplementary Figure S.2: Violin plot comparing trait values between species at the end of the historical climate forcing a-c) and global warming forcing b-d) per trait and species. The horizontal line within each violin is the median.



SUPPLEMENTARY FIGURE S.3: : Effect of the different trade-offs on the evolution of temperature optimum under global warming conditions. Solid lines are the mean across species while dashed lines are their standard deviation. Each scenario is detailed in S.1



SUPPLEMENTARY FIGURE S.4: : Effect of the different trade-offs on the evolution of the generalist/specialist trait under global warming conditions. Solid lines are the mean across species while dashed lines are their standard deviation. Each scenario is detailed in S.1



SUPPLEMENTARY FIGURE S.5: : Fitness landscape per species (with $\chi = 10$) during four different periods, before and during global warming. The average individual spawn output throughout lifetime of a cohort of one phenotype within one species is used as fitness proxy. The landscapes are generated using the K-kernel nearest neighbour smoother on the fitness values of all phenotypes across simulations. The dashed lines in each column shows the average temperature during that period of time (the value is different in each column).

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